SOME PTERIDOSPERM STEMS AND FRUCTIFICATIONS WITH PARTICULAR REFERENCE TO THE MEDULLOSAE[1]

ROBERT W. BAXTER[2]

INTRODUCTION

Theophrastus, one of the first to attempt the classification of plants, recognized as his major groups, trees, shrubs, and herbs. Although this division was long ago realized to be an artificial one it nevertheless provided then, as it does today, convenient categories for different types of plant habit. Since the study of paleobotany involves not only the search for the ancestral types of present-day plants but also attempts to visualize and illustrate the gross appearance of past floras we may still find it convenient to use these major habit groupings in classifying fossil plants.

We now know that the Carboniferous forests were made up of the tree-like *Pitys, Cordaites, Lepidodendron, Sigillaria* and *Calamites,* which attained diameters of several feet and reached 100 feet or more in height. Growing among these trees were numerous plants of creeping, climbing, and shrubby habit, characterized in general by small stems with little or no secondary growth. It is also generally true that this last group (ferns and seed-ferns) had developed large leaves or fronds (megaphyllous) while the larger tree-like plants were generally small-leaved (microphyllous). The term "microphyllous" is used in this paper in a broad sense to include not only the groups lacking leaf gaps but also those living and fossil gymnosperms (Coniferophyta, Arnold, 1948) in which the seeds are stem-borne (Sahni's (1920) Stachysperms) and the leaves are small, simple, linear or fan-shaped growths, borne in dense spirals or whorls on the trunk and branches.

In plant evolution the early development of a single large trunk (tree-like) seems to have some correlation with microphyllous habit, as the development of numerous small branches of equal size (shrubby) may be correlated with megaphyllous form. Accordingly, it seems possible that a classification based on external form and size may, considered in relation to the origin of plant groups, not be entirely without some phylogenetic meaning.[3] As might be supposed, the larger tree-like fossils

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[2] Assistant Professor of Botany, University of Kansas, Lawrence.

[3] While it is not our present intention more than to suggest the possibility of the foregoing statements, there is ample evidence that the Coniferophyta (Ginkgoales, Taxales and Coniferales) have been trees and microphyllous since their origin from the Pityeae and Cordaiteae in Upper Devonian and Carboniferous times (Arnold, 1948). The other groups of Carboniferous trees *(Calamites, Lepidodendron,* etc.*)* are, on the other hand, represented today by only a few isolated genera in the so-called fern allies. Thus it would seem that the only possible ancestral forms of the megaphyllous gymnosperms, and possibly the angiosperms, must be sought in the shrubby, climbing or herbaceous undergrowth of the Paleozoic forests. In this habit group through profuse equivalent stem ramifications the *telome* units would be provided for the development of the large frond and broad leaf, which when fertile may have evolved into sporophylls or carpels (Wilson, 1942).

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have received a proportionate amount of attention and are today relatively well known. On the other hand, while numerous genera and species of the smaller plants have been discovered and described, it is becoming increasingly apparent that the field is open for the discovery of many more. This is due in part to improved techniques and increasing amounts of research material but probably even more to the undoubted greater diversity of the smaller plants. Certainly in many forest areas today, the genera and species of tree-like habit are but a small fraction of the total flora as compared to those of associated shrubs and herbs. In the present paper we intend to deal with some of these newly discovered small plants (or plant organs) which appear to be of pteridosperm affinity.

As is well known to all paleobotanists, the fragmentary nature of the material preserved in coal balls makes it necessary to describe the isolated plant organs (stems, roots, leaves, fructifications, etc.), with the hope that subsequent work will show their proper assemblage. Thus the seed-ferns as a group were originally described as the Cycadofilicales on the basis of stem anatomy, which seemed to combine both fern and cycad characters along with a constant association with fern-like foliage. It was not until 1905 that seeds were actually found attached to some of these fronds and the present conception of the groups was created. Even now the possession of seeds is definitely known for only the genus *Lyginopteris (Calymmatotheca Hoeninghausi)* and can only be inferred for the numerous other stems which have been carried over into the new classification on the basis of their similar anatomy. Briefly, the characters on which this relationship is based are: small stems, pith or mixed protostele with exarch or mesarch primary wood, secondary wood of characteristic angular (in cross-section) tracheids, reticulate-bordered pitting, usually numerous leaf traces, and an outer cortex containing vertical or horizontal sclerotic bands. Additional similarities and differences are shown in the accompanying table which lists most of the better-known pteridosperm stem genera.

Our new genus (page 289) is validly included through possession of most of the above-listed characters although it lacked leaves and may or may not have had seeds. Its reconstructed habit (plate 5) does, however, show a close flattened branching pattern which offers implications as to the possible megaphyllous development of large fern-like fronds. Such ramification in a single plane, along with the lack of leaves, is suggestive of the Psilophytales, and it is our opinion that *Microspermopteris* may constitute a direct link between that primitive group and the larger seed-ferns. The constant small size (5 mm. or less) of its stems indicates that it would at best have been an inconspicuous element of the forest group and must have been either prostrate or climbing.

The three new species of *Medullosa* described are of course generically identifiable by their polystelic structure as well as by the character of the wood and pitting and, where the latter tissue is preserved, by the fibrous cortex. Here again the evidence of size and form seems to indicate that the habit was either creeping or climbing rather than tree-like.

The two new species of *Dolerotheca* are offered primarily as a supplement to Schopf's (1948) comprehensive work on the genus, although we believe our material does present some basis for additional phylogenetic interpretation as well as possible additional support for the more definite connection of the fructification to the Medullosae.

During the latter course of this study several additional small stems of apparently primitive pteridosperm character have been discovered which we hope to describe in a future paper. One in particular is of interest since, as in *Microspermopteris*, it appears to be leafless. Thus at least a part of the undergrowth of Carboniferous times seems to have occupied a position comparable to that of the living fern allies in that both present a retention of characters primitive for their time so that the excellent fossil record of the coal beds may yet provide the missing links from earlier eras just as those primitive living genera *(Lycopodium, Equisetum* and *Psilotum)* have done in part for the present-day flora.

Microspermopteris aphyllum, gen. et spec. nov.

The following description is based on a total of eight stems occurring in three different coal balls. Four stems were followed through one coal ball for approximately 6 cm. and three stems extended through another ball for approximately 4 cm. The eighth stem was isolated in the third coal ball and was cut as a longitudinal section 1 cm. in length.

All material is from the What Cheer Clay Products Co. coal mine, one-half mile west of What Cheer, Iowa. This horizon lies in the Des Moines series of the Pennsylvanian and is accordingly of Upper Carboniferous age.

The stems followed a relatively straight to slightly sinuous course. Mixed among them were numerous specimens of their smaller, but otherwise identical branches. The stems are of a constant small size even when maturity is indicated by considerable secondary growth. The total diameter including cortex and epidermal tissues never exceeds 5 mm., while the single stele averages 2 to 2½ mm.

The external form of the stems is quite variable, particularly in the smaller specimens where the transverse configuration is almost "amoeboid" in outline (fig. 3). The more mature specimens with considerable secondary growth appear oval to circular in cross-section (figs. 1 and 7).

The primary tissues consist of a protostele in which the large metaxylem tracheids are divided into groups of 12–14 cells by a radiating network of parenchyma, the individual strands of which are usually not more than one cell in thickness and in longitudinal section are seen to be vertically elongated cells, five to six times as long as wide. The inconspicuous protoxylem groups are situated on the periphery of the primary tissue and appear to be exarch though their exact position is vague due to the very small size of the adjacent innermost secondary wood. The metaxylem tracheids increase slightly in size towards the center, averaging 150 μ in diameter as against 50 μ for the secondary wood. All walls of the metaxylem are reticulately bordered pitted with the opposing orifices at a slight angle to one another (fig. 12).

Comparative characters of seed-fern stem genera	Approximate number of steles and stem diameter	Primary wood	Secondary wood and ray structure	Cortex	Leaf traces and petiole	Horizon
Microspermopteris	Single stele Stem: 5 mm.	Exarch; a nearly solid to mixed protostele divided into groups of 12–14 cells by parenchyma network	Secondary wood usually well developed, increasing in size towards outer layers; pitting reticulate-bordered. Rays few, low, uniseriate.	2-zoned; inner zone homogeneous; outer zone with a vertical series of horizontal sclerotic plates	Leaf traces lacking; branch traces concentric and indentical to stele; branching at right angles to stem	Des Moines Series, Pennsylvanian
Lyginopteris	Single stele Stem: 2–4 cm.	Relatively large pith; sclerotic nests with marginal strands of mesarch primary wood	Secondary wood often well developed, interrupted by leaf traces. Rays wedge-shaped, wider towards outside	Inner cortex with sclerotic nests and secretory cells. Outer cortex with anastomosing vertical sclerotic bands; spinous emergences	Leaf traces originate in primary wood on pith margin and pass out through gaps in secondary wood; divide into 2 in cortex and fuse V-shaped in petiole	Carboniferous
Heterangium	Single stele Stem: 1–2 cm.	A mixed protostele, usually mesarch	Secondary wood seldom more than 8–10 layers thick; reticulate-bordered pitting. Rays broad, often wedge-shaped	2-zoned; inner zone with horizontal sclerotic bands; outer zone with vertical sclerotic bands	Leaf traces originate as 1 or 2; always dividing into 4–8 in the petiole	Lower Carboniferous to Permian
Rhetinangium	Single stele Stem: 2 cm.	Exarch; a mixed protostele with very large metaxylem cells and parenchyma with secretory cells	Secondary wood with reticulate-bordered pits on radial walls. Rays broad and high	Inner cortex lacking sclerotic tissue; outer cortex with vertical sclerotic bands	4–5 U-shaped traces with exarch protoxylem form a single corrugated band. Petiole base larger than main stem	Lower Carboniferous
Medullosa	2–8 steles Stems: 2–12 cm. (excl. Permian species)	A mixed protostele with large metaxylem cells. Protoxylem usually exarch	Secondary wood usually with greatest growth towards stem center. Rays thin (1–2 cells) and 1 cm. or more high	Containing numerous collateral leaf traces and resin canals; outer cortex with vertical sclerotic bands	Leaf traces collateral, very numerous. Petioles large with numerous traces	Lower Carboniferous to Permian

Comparative characters of seed-fern stem genera	Approximate number of steles and stem diameter	Primary wood	Secondary wood and ray structure	Cortex	Leaf traces and petiole	Horizon
Sutcliffia	1 large central stele surrounded by small subsidiary strands (meristeles) Stem: 12 cm.	Exarch; a mixed protostele with large metaxylem cells and parenchyma with secretory cells	Secondary wood weakly developed (3–4 rows). Rays thin (1–4 cells), 1–2 cm. high	Outer cortex with vertical sclerotic bands similar to *Medullosa*	Traces concentric, numerous, arising from meristeles. Petioles similar to those of *Medullosa*	Lower Carboniferous
Stenomylon	Single stele Stem: 2 cm.	Triangular mixed protostele; parenchyma bands running from 3 corners to center	Secondary wood well developed; reticulate-bordered pitting on radial walls. Rays broad and wedge-shaped	Inner cortex lacks sclerotic tissue; outer cortex with vertical sclerotic bands	Leaf traces originate from corners of triangular protostele and divide into numerous bundles	Late Devonian and Lower Carboniferous
Calamopitys	Single stele Stem: 2–5 cm.	A pith with endarch primary xylem or a mixed protostele	Secondary wood often well developed (20–30 rows); reticulate-bordered pitting on radial walls. Rays broad	Outer cortex with vertical sclerotic bands similar to *Medullosa*	Leaf traces often concentric, leave stele as 1 or 2 and divide into 6–8 or more in the petiole which resembles that of *Medullosa*	Late Devonian and Carboniferous
Aneurophyton (*Eospermopteris*) (see footnote, p. 294)	Single stele Stem: 1–2 cm., although 3-ft. stump casts are recorded	Triangular protostele, exarch with protoxylem at the 3 angles	Abundant secondary wood; reticulate-bordered pits on radial and tangential walls. Rays small, thin, 1–2 cells wide	Outer cortex with scattered vertical sclerotic strands	Leaf traces lacking; branch traces similar to main stele but smaller	Middle Devonian
Schopfiastrum	Single stele Stem: 2 cm.	Exarch; a mixed protostele	Secondary wood well developed; reticulate-bordered pits on radial walls. Rays thin and high	Resin canals rare or absent; outer cortex with vertical sclerotic bands	Leaf traces large, bilobed, in opposite pairs	Des Moines Series, Pennsylvanian

The secondary wood ranges from 3–4 rows in thickness in the young small stems to around 16 in the larger more mature specimens. The first-formed cells are quite small, being hardly distinguishable in size from the protoxylem. Their diameter increases gradually towards the outside but never approaches that of the metaxylem. Longitudinal sections of the secondary tissue show the radial walls pitted in the same way as the metaxylem, with a dense reticulum of bordered pits, while the tangential walls have fewer scattered pits, with more lineal openings, arranged in irregular rows up and down the central area. Wood rays are inconspicuous and relatively sparse. They are small, uniseriate and from 1 to 4 cells in height (fig. 9). A rather frequently observed character of the secondary wood of the mature stems is its unequal development (fig. 7) which is possibly due in some cases to differing cambial activity and in others represents the unfilled gaps left by departing branch steles. The tissues immediately surrounding the wood are seldom well preserved and are represented in all of our specimens as merely a thin dark brown ring of crushed cells. There is no evidence of periderm formation.

The cortex is divided into an inner and outer zone of approximately equal thickness. The inner part is composed of poorly preserved isodiametric thin-walled cells containing numerous, scattered dark secretory cells. The outer zone is thicker-walled and usually better preserved, consisting of a compact tissue of brick-like cells (hexagonal to circular in transverse section), about twice as long as wide, the elongation being parallel to the axis of the stem. This merges into an outermost tissue which is 2–3 cells thick and differentiated by being made up of cells four to six times as long as broad. An unusual character of this tissue is the frequent occurrence of multicellular emergences which are commonly broad at the base, tapering to a sharp point. They are sometimes forked and horn-like (figs. 5 and 55) and may occur singly or in clusters (fig. 8). In length they average .6 mm. There is no evidence that they were glandular like the emergences of *Lyginopteris*, nor do they appear to have been arranged in parallel rows as has been described for the latter genus (Scott, 1923). On the contrary, they are produced more or less indiscriminately with the exception that they are nearly always present at the point of departure of a branch.

A feature of the outer cortical zone which is probably the most unique in relation to the comparable pteridosperm genera is the presence of a vertical series of *horizontally* aligned sclerotic plates instead of the usual vertical strands. These consist of thick-walled stone cells, 2–4 cells deep and 4–6 cells in diameter (fig. 10). In tangential section they are occasionally seen to anastomose with adjoining plates at the same level and with plates above and below, thus appearing as a loosely arranged horizontal network (fig. 11).

One of the most difficult problems in interpretation has been the question of whether *Microspermopteris* bore leaves. As stated earlier, we have followed four of the stems for approximately 6 cm., three for 4 cm., and another for about 1 cm.

This produced a close check on nearly 37 cm. of stem, all, of course, not of the same plant. However in this rather respectable amount of material we encountered only five instances of vascular tissue being given off from the main stele. In every case the details are identical and are illustrated for both a young and mature specimen in figs. 1, 2, 3, 5 and 55.

The branch is first evident as a departure from the stele of a complete segment of primary and secondary wood, with the crushed phloem and cambium tissues on its outer, abaxial surface. At this point it consists of 8 to 12 metaxylem cells with possibly 1 to 2 strands of protoxylem, bordered on the outer side by almost the complete amount of secondary wood present at that particular point on the main stele. This results in a conspicuous gap being produced in the mature stems and a relatively smaller one in the young stems where the proportion of secondary growth is much less. The angle of departure is acute (around 30°), the trace following this steep course through the cortex for approximately 2 to 3 mm. During this space the secondary wood and enclosing parenchyma tissues completely surround the primary core and produce a concentric bundle identical to the main stele except in size. The bundle then turns sharply outwards and proceeds at right angles to the stem axis for a distance approximately equal to the normal diameter of the stem before again resuming an upward course. As shown in fig. 5, the branch, where it projects horizontally out from the stem, almost equals the stem in size and exhibits all of its characteristic sclerotic plates and cortical zones. At no time does the bundle show any tendency to subdivide further, while a transverse section of one of the branches at a point around 4 mm. from the main stem shows it initiating a further small branch of its own in the same plane as the primary one. The branching was apparently distichous at relatively long intervals, so that the habit was probably fairly close to the partial reconstruction shown in pl. 5.

Adventitious roots, which are primarily limited to the axis of the branches, are similar to those of *Lyginopteris.* They are commonly hexarch or heptarch with conspicuous protoxylem groups at the points of the projecting arms (fig. 4). The phloem lies between these arms and, as in *Kaloxylon,* there is a small amount of conjunctive parenchyma in the metaxylem. The stele is enclosed by a single poorly preserved dark ring which probably represents the endodermis. The cortex is homogeneous and identical to the inner cortical zone of the stem. The peripheral zone is undifferentiated, so that in transverse section the loosely packed cortical tissue with scattered secretory cells appears to extend clear to the edge of the irregularly lobed outer margin. This lack of a differentiated epidermal zone is one of the distinguishing features between these roots and those of *Lyginopteris.*[1] Secondary growth is rather rare but when present is again similar to that of *Kaloxylon,* cambial activity initiating in the depressions between the protoxylem

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[1] While the information in the literature is often vague on this point, similar roots have also been described for *Heterangium,* although they are usually listed as diarch or triarch (Scott, 1923).

points and producing wedges of typical secondary wood alternating with wedge-shaped rays opposite the protoxylem. The pitting is identical to that of the corresponding tissues in the stem. As might be expected, the roots are of constant small size, with the most mature specimens showing 6–7 layers of secondary growth not exceeding 2 mm. in total diameter. The point of their insertion on the stem offers another similarity to *Kaloxylon* as roots are most frequently found immediately above the branch attachment (see Scott, 1923, p. 49) where their horizontally departing bundle seems to function, in part, in filling up the branch gap. As it has been possible to follow these roots from their insertion on the stem (fig. 6) out to typical transverse sections as in fig. 56, their identity is beyond doubt.

Discussion:

At first glance, in transverse view *Microspermopteris* presents a close resemblance to *Heterangium*. The size is comparable to *H. minimum* (Scott, 1917), and the primary wood with its thin network of parenchyma separating large groups of tracheids is more closely approximated by *H. Kukuki* (Hirmer, 1933) although the total amount of parenchyma is much less in *Microspermopteris*. In the anatomy and insertion of the roots and the presence of multicellular emergences on the stem and branches we have structures comparable to *Lyginopteris*. However, the almost solid protostele contrasts with that of *Lyginopteris*, while the absence of leaf traces and of a vertical fibrous hypoderma, along with the exarch position of the protoxylem, removes all possibility of assigning the specimens to *Heterangium*.

While the horizon of our petrifactions is late Upper Carboniferous and *H. Grievii* Scott is of Lower Carboniferous age, there seems little doubt but that we are dealing with a more primitive plant which possibly represents the ancestral stock of *Heterangium*. In fact, if it were possible to increase slightly the amount of parenchyma in the primary wood, fuse (through webbing) the closely grouped parallel branches into a multi-bundle rachis (Lignier's (1908) theory of megaphyllous development), and add a hypodermal zone of vertically elongated fiber bands we would have a stem quite similar to *Heterangium*. The sclerotic plates lying in the extreme outer cortical zone of *Microspermopteris* (fig. 10) are in radial view somewhat similar to the plates found in the middle cortex of all of the *Heterangium* species (with the exception of *H. minimum* which, according to Scott, lacks fibrous and sclerotic tissue altogether).

The most obviously primitive and unusual feature, the leafless condition, can be assumed to be demonstrated since our material permitted examination of approximately 37 cm. of different stems. The only similar character in plants of possible pteridosperm affinities is in *Eospermopteris (Aneurophyton)* of the middle Devonian.[1] We must assume, then, partly on the lack of any intervening evidence, that we are dealing with a link leading the pteridosperm complex clear back to the

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[1] Although the fructifications originally described as seeds were later shown to be sporangia the anatomy of the stem still provides some basis for including the genus in the pteridosperms.

Psilophytales. Indeed, Dawson's restoration of *Psilophyton princeps* (known only from compressions) is disturbingly similar to our own restoration of *Microspermopteris,* particularly in the flattened branching pattern and the presence of spine-like emergences on the stem. Since what we know of *Psilophyton* stelar structure indicates that it possessed only spiral and scalariform pitting there obviously cannot be any direct comparison in internal anatomy with that of the secondary wood and highly developed bordered pitting of *Microspermopteris.* However, the gross appearance is close enough to intimate that a compression form of M. *aphyllum* might be identified as a *Psilophyton.* The middle Devonian genus *Schizopodium* offers a closer parallel in pitting and beginning of secondary growth. However, we consider it here just an example of the early, contemporaneous origin of these characters in contrast to the more conventionally primitive scalariform pits and solitary primary tissues, since the present evidence indicates its relationship to the Cladoxylaceae rather than the Pteridospermae.

In Andrews' (1940) account of the stelar anatomy of the pteridosperms he makes the following observation:

> . . . it should be stated that the view that the pteridosperms represent an intermediate group between the ferns and cycads is no longer tenable. Rather we must look to a common psilophytalean-like ancestor with terminally borne sporangia, a solid protostele and primitive secondary wood for the origin of the ferns and pteridosperms . . .

While we are more inclined to feel that the ferns arose independently, in many ways our present genus fulfils the theoretical requirements outlined.

The possibility that M. *aphyllum* was parasitic and its leafless condition a result of degeneracy rather than primitiveness has not been overlooked. The fact that the habit was probably epiphytic (climbing) or prostrate in a swamp humus tends to lend some weight to such a view as does the apparent absence of stomata and potential photosynthetic tissues. However, since no organs resembling haustoria are present and the roots resemble so closely the aerial ones of *Lyginopteris* we cannot consider a parasitic condition too seriously. At the same time the combination of so many characters common to both *Lyginopteris* and *Heterangium,* along with the more primitive stelar structure and lack of differentiation into rachis and lamina, seems to point rather definitely to an ancestral form from which both genera may have developed independently. This conflicts with Scott's (1923) theory of *Lyginopteris* arising from a developmental series through the subgenus *Lyginangium,* and it may be necessary to reconsider some of Kubart's transitional *Heterangium* species as being actually primitive *Lyginopteris* species leading back to *Microspermopteris.*

Since no seeds or any fertile parts whatever have been found, it is necessary to include *Microspermopteris* among the numerous other organ genera assigned to the seed-ferns on purely anatomical characters. It may be open to question whether in its leafless condition it could have borne seeds. If they were present they were more than likely terminal on the smallest branch divisions. However, there is no reason for not considering the possibility that the stem anatomy constituting the organ genera of pteridosperms did not precede the development of seeds (i.e. *Eospermopteris (Aneurophyton)*. Certainly in many of the Devonian and Lower Carboniferous Calamopityaceae the presence of seeds is still to be proven, although the degree of differentiation into stem and leaf-bearing organs had obviously reached a more advanced stage than that shown by *Microspermopteris.*

It can be hypothesized that certain small psilophytalian plants struggling for survival in an environment of increasing lushness and density might well have developed a vine-like habit, involving additional conductive stelar tissue as well as supporting sclerotic and fibrous zones, to be followed chronologically by differentiation into leaves (as a more efficient light-catching mechanism) and still later by seeds as a product of the changing and possibly drying environment. Viewing evolutionary change as a response to environmental change, it is difficult to see seed production ever replacing reproduction by spores if there had not been a constant impetus to survival under conditions unfavorable (lack of proper moisture) to spore germination. It also seems likely that the struggle for living space and light preceded the above conditions.

From the original psilophytalian stock larger and anatomically more complex forms would arise independently, leading by gradual ecological adaptations to the recognized groups of Carboniferous plants. Certainly, the contemperaneous association, even as early as the Upper Devonian period, of widely differing stelar structures for the ferns and pteridosperms would seem to indicate that they had a separate individual origin. Some of the earliest known forms assigned to the ferns such as *Arachnoxylon* and *Reimannia* of the Upper-Middle Devonian show definite affinities to the Carboniferous Zygopteroideae, while *Eospermopteris* of about the same age shows many seed-fern characters *in spite of apparently producing only spores.* Thus, although the picture is complicated by the existence of numerous genera from compressions of which we have no knowledge of the internal anatomy (i.e. *Archeopteris,* etc.), the safest and most consistent distinction between the two groups would seem to be stelar structure. Using this as a criterion, it would be possible to have a phylogenetically correct classification including, on the one side, pteridosperms, having only terminal sporangia and, on the other side, ferns exhibiting heterospory. There certainly can be no reasonable objection to recognizing that the seed-ferns must have passed through a sporangiate stage or that ferns may not have achieved heterospory as a terminal development rather than as a stage in seed production.

The designation of the group as Pteridospermae becomes increasingly unfortunate if we recognize their independent origin from the Psilophytales and the fact that the most primitive genera undoubtedly lacked seeds. The same situation has been dealt with in the Lepidodendrales (i.e. *Lepidocarpon* vs. *Lepidostrobus*) with much less confusion. Here the general plant structure and anatomy have been accepted as the basis for the order, while seed production has been recognized as an advanced stage of heterospory within certain species and genera. For some reason it has never seemed necessary to create the Lycopsidospermae to include *Lepidocarpon* although considered on the same basis as the pteridosperms such should be the case.

The following seem to the author to be the important points to bear in mind in relation to Pteridospermae in question.

(1). They are psilophytalian in origin rather than arising from the ferns.

(2). They are possibly of dual origin, with *Eospermopteris* leading to the Calamopityaceae complex and *Microspermopteris* leading to the *Lyginopteris* and *Medullosa* complex.

(3). Leaves *when present* are large and fern-like; seeds *when present* are basically terminal.

(4). The stem and petiole anatomy is constant and characteristic enough to delimit clearly the group irrespective of known possession of seeds.

(5). Included on the basis of the above anatomical criteria are genera such as *Microspermopteris,* which may or may not have had seeds, and *Eospermopteris,* in which the possession of seeds seems doubtful.

(6). While genera known only from compressions such as *Archeopteris* may be links in the pteridosperm chain, they are just as likely, in the absence of anatomical evidence, to be true ferns. Heterospory, as shown by the modern genera *Salvinia* and *Marsilia,* as well as the fossil lycopods, does not necessarily always imply later seed development.

(7). Seed development in the pteridosperms may in some isolated cases have preceded the differentiation of fern-like leaves with the seeds being borne terminally on naked branches. In other words, we are possibly dealing with early seed-plants which through parallel evolution developed fern-like leaves rather than, as originally thought, with ferns which developed seeds. The distinction may seem trivial, but while the original premises are close the phylogenetic conclusions (depending on which starting point is selected) are quite distinct. The terminal position of the seed in *Lyginopteris oldhamia* and *Aneimites fertilis* are cases in point since these species are among the oldest forms in which seeds are known.[1] (We can only hope that the discovery of fertile material of *Microspermopteris* will illuminate this point.)

Diagnosis:

Stems of constant small size, the stele never exceeding 2.5 mm. or the entire stem 5 mm. *Metaxylem* of large cells (150 μ diameter), diminishing towards the

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[1] While these seeds are "terminal" on leafy fronds rather than on naked stems it seems not unlikely that their apical position involves a carry-over from a developmental stage prior to the acquisition of leaves.

periphery. Protoxylem exarch, of numerous indistinct groups. Xylem parenchyma arranged in a thin network enclosing groups of 12 to 14 metaxylem cells. *Secondary wood* of small angular (in cross-section) tracheids from 3 to 16 layers in thickness, increasing in size towards the outer edge. Reticulate-bordered pitting with crossed orifices in the metaxylem and on radial walls of the secondary wood. Scattered bordered pits with lineal openings on tangential walls. Protoxylem spiral or annular. Rays rare or lacking; when present, small, uniseriate, 1–4 cells high. *Cortex* differentiated into inner and outer zones. The inner zone composed of isodiametric thin-walled cells, poorly preserved, with scattered secretory cells but lacking sclerotic tissue. Outer zone of thicker-walled, longer cells containing vertical series of horizontal sclerotic plates. *Epidermis* of similar but more elongated cells producing numerous multicellular pointed emergences. *Leaf traces* lacking. Branching distichous and at right angles to the stem. *Roots* adventitious, hexarch to heptarch, commonly inserted above point of branch departure.

Horizon: Des Moines Series of Pennsylvanian.

Type: fig. 1. Slide 1602 in the paleobotanical collection of the Henry Shaw School of Botany of Washington University.

SOME NEW AMERICAN MEDULLOSAS

In the interval since Thiessen (1920a, 1920b) discovered and identified a pteridosperm stem as *M. anglica* (later to be assigned varietal distinction by Schopf, 1939) three new species and one variety of *Medullosa* from American coal balls have been brought to light. They are: *M. Noei* (Steidtmann, 1937), *M. distelica* (Schopf, 1939), *M. Thompsonii* (Andrews, 1945), and *M. anglica* var. *ioensis* (Andrews & Kernen, 1946). With the exception of *M. Noei* all of these new species and varieties have formed a fairly closely integrated group assignable to the subgenus Anglorota along with the European species *M. anglica*, *M. centrofilis*, and *M. pusilla*. *M. Noei*, showing affinities with *M. Leuckarti*, is held to be transitional between the Carboniferous form cycle and the Permian species.

Our knowledge of this very interesting group has been expanding rather rapidly, and with the hope of throwing still further light on the subject three new species of *Medullosa* are herewith described and additional new data are presented on *M. Noei*.

Medullosa primaeva, sp. nov.:

The following description is based on a single coal ball specimen from the Urbandale Mine located 1.2 miles west of Des Moines, Iowa, on U. S. Highway No. 6. This is the same location from which Andrews (1945) described *M. Thompsonii*. The horizon is the Des Moines Series of the Pennsylvanian. The material was collected and cut by Mr. Frederick O. Thompson of Des Moines, who generously donated it to the Henry Shaw School of Botany of Washington University. It consists of a cut block 5.5 x 5.5 cm. and 1.3 cm. thick, with the stem exposed on one side through a fracturing away of the adjoining material. The stem's course is through the thickness of the block at a slight angle from the vertical, the total available length being 1.4 cm. Figures 14 and 15 show the appearance of the top and bottom surfaces of the specimen prior to any grinding of the fractured edge. Approximately one half of the cortex and external tissues have been lost on the side of the fracture, though the multiple stele appears to be nearly intact.

As shown in fig. 14, the upper[1] surface of *M. primaeva* exhibits 5 rather large and uniform-sized steles, 2 of them partially fused. There are also 2 small steles and a portion of a third on the fractured margin. The lower surface shows the same 8 steles, though somewhat altered in orientation and size, with 3 of the steles partially fused. It is not implied, however, that 8 was the constant number of steles as even in the short length of stem available stelar fusions and divisions were numerous and the diversity of vascular growth even included the production of steles running horizontally through the stem for short distances (fig. 13). Still, even with these variations the stele number seems to have been constantly 6 or more.

The stem measures 2.0 cm. in diameter, the individual steles ranging from around 5 mm. for the average large ones to .5 mm. for the very smallest. The 5 largest steles are closely comparable in size to those of *M. Thompsonii* even though the stem of the latter is considerably larger, averaging 3.5 cm. in diameter. The steles are essentially radially symmetrical with a very slight tendency towards endocentricity.

It may be argued that some of the smaller vascular strands (fig. 14, S3 and S8) do not constitute true steles. However, even the smallest possesses 8 or more layers of secondary wood and can be seen to be independent in its course throughout the entire length of the specimen (fig. 13). Neither can they be designated as accessory strands from which leaf traces might be produced (as in *Sutcliffia* and *M. anglica*) since the two largest of the 8 steles are, in our specimens, the sole observed source of trace departure.

The primary wood is small in amount and is characterized by the almost complete absence of parenchyma; what little there is being restricted to a thin network running through or enclosing the primary cylinder, from which the high uniseriate rays extend out through the secondary wood. The primary wood forms a cylindrical to irregularly shaped core around which it is often difficult to determine the exact inner limits of secondary growth. The protoxylem is not distinguishable (figs. 14 and 19).

The secondary wood is variable as to cell size and radial growth, the first-formed layers being often composed of large tracheids (similar in size to the metaxylem) which merge some distance out into rows of much smaller cells. On

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[1] The interpretation as to lower and upper surfaces of the stem is made on the basis of the outward passage of leaf traces exposed in a series of longitudinal peels.

the other hand, the same stele may, on the opposite side, show the first-formed secondary wood to consist of very small (in diameter) tracheids and the successive outermost cells to be large (fig. 19).

Each stele is enclosed by a dark tissue of crushed cells, probably of cambium and phloem, in which are occasional small resin canals. The entire stelar assembly is surrounded by a very thin, parenchymatous "periderm" which is never over 2 to 3 cells thick and is often so poorly preserved as to be indistinguishable from the cortex.

The rays are up to 1 cm. or more in height and apparently constantly uniseriate. In this regard they probably come closest to Andrews' (1940) classification II B in which he originally placed all of the Anglorota group as well as *M. Noei* and *M. Leuckarti.*

The cortex is composed of cells rounded in transverse view but elongated vertically two to three times their width. Traversing upward and outward through the cortex are numerous small collateral leaf traces consisting solely of 3–4 protoxylem tracheids with spiral thickening (fig. 27) and an abaxial phloem group. There is definitely no secondary wood associated with the trace. Mucilage canals with their "resin rodlets" are scattered sparingly through the cortex and are unusually small, having a constant diameter of less than 60 μ. They are commonly closely associated with the leaf traces and, in contrast to the majority of the other American species, seem to have seldom invaded the hypodermal, sclerotic strand zone.

The sclerotic strands form a single layer and in transverse view appear circular to slightly radially elongated. They are separated by 2–3 layers of cortical-like cells from a conspicuously darkened epidermis. This latter tissue consists of brick-shaped cells with a slight tangental elongation and rather thick walls which occasionally show evidences of a cuticle.

Discussion:

Our specimen shows a rather close similarity to *Medullosa Thompsonii* in the secretory canals—their small size, their comparative scarcity in the stem as a whole, and their almost complete absence in the sclerotic fibrous zone. However, although Andrews (1945) points out that the number of steles in the Medullosae is generally an unreliable taxonomic character (stelar divisions and fusions often resulting in variations of 2–3 or more steles), the possession by *Medullosa primaeva* of 7 to 8 steles, which tend to pursue horizontal courses through the stem and almost completely lack conjunctive primary parenchyma, clearly makes it of specific importance and distinct from *M. Thompsonii.*

Medullosa centrofilis and *M. pusilla* are the only other species which seem similar enough to deserve consideration. The former comes closest to *M. primaeva* in number of steles (considering the "star ring" as a fourth stele) but lacks the horizontal stelar meanderings and exhibits many more and larger secretory canals. *M.*

pusilla is comparable in over-all stem size but again is separated by the stele number, the difference between 3 and 7–8 being held as more than specific variation.

The slight tendency toward endocentricity of the secondary wood and paucity of conjunctive parenchyma in the primary area, along with its generally netted arrangement, make the individual steles more closely comparable to those of *Microspermopteris* than to *Heterangium*. According to Bower's (1930) "size and form" principles one would expect relatively little parenchyma in steles of such small size, but comparison with the equally small stele of *M. Thompsonii* seems to show greater differences than can be accounted for on the basis of Bower's hypothesis. Thus although the *M. primaeva* stelar number is much larger than in any of the other species of equivalent age the general stele structure appears to be more primitive. This is in contrast to what might be considered advanced development as evidenced by the absence of secondary wood in the leaf traces and leads one to believe that the presence of such secondary wood in *M. anglica* is not necessarily indicative of a primitiveness either for the character or the species as a whole. On the contrary, it seems most logical at present to consider *M. primaeva* with its numerous small, radially symmetrical steles as having developed from a monostelic stem through stelar proliferation and accordingly representing a primitive stage of the genus.

The specific name *primaeva* has therefore been assigned.

Diagnosis:

Stem small, not exceeding 3 cm. Steles numerous, 6–8, frequently fusing and dividing, ranging from .5 to 5 mm. in diameter, often pursuing a sinuous horizontal course through the stem. Primary wood parenchyma small in amount or lacking. Resin canals small and few, almost entirely absent from fibrous hypodermal zone. Rays uniseriate; secondary wood of variable cell size; irregular radial growth, only slightly endocentric.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 14. Slide 1615 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Medullosa elongata, sp. nov.

The following description is also based on coal-ball material collected by Mr. F. O. Thompson and his associates of Des Moines, Iowa. The source was a large open pit mine of the Atlas Coal Co. located in Wilson County, Iowa. The horizon is Pennsylvanian, Des Moines Series.

The greater part of material from this locality was too heavily pyritized to permit good plant preservation, but the stem fragments which were identifiable indicate a flora consisting primarily of *Lepidodendron* and *Calamites*. Pteridosperms were relatively rare, the present description being based on a single stem specimen 7 cm. long and 6 x 1.5 cm. in diameter. There evidently had been some crushing, which would account partially, but not altogether, for the asymmetry (fig. 16).

The outstanding feature of the three steles is their extreme endocentricity in which character they resemble Schopf's (1939) *M. distelica.* The steles maintain their individuality, i.e., no stelar fusion, and relative position throughout the 7 cm. of stem length with the endocentric secondary development also showing a constant approximate 4 to 1 ratio in thickness as compared to the exocentric secondary tissues. The three steles are of equal size, averaging 10 × 2 mm., the plane of elongation following that of the stem as a whole and constituting a factor in the evidence that the general asymmetry was a natural character of the living plant. Two of the steles occupy a position directly opposite one another and near the center of the stem while the third is isolated off to one side (fig. 17). The primary xylem consists of a long narrow area following the elongation of the stele. It is seldom over 2 cells in width and runs up to 8 mm. in length. The metaxylem tracheids are large (.2 mm.), and usually triangular in cross-section. There is relatively little conjunctive parenchyma, while the protoxylem is indiscernible.

The secondary wood is rather unusual for a *Medullosa* in that the majority of the cells are square in transverse view, while the others are of the more characteristic alternately arranged pentagonal shape. Also, in contrast to the somewhat similar *M. distelica,* the radial rows of secondary tracheids are not conspicuously divided by rays nor are the outermost cells differentiated. In addition, the rays are uniseriate, not particularly numerous, and almost impossible to detect in transverse view.

Surrounding each stele is a thin dark layer of crushed cells containing numerous small resin canals. The periderm is thin (3–4 cells), poorly preserved, and apparently interrupted at the narrow ends of the steles where the leaf traces are given off. The cortex is rather poorly preserved due to pyritization, with numerous rather large slime canals (.2 mm. in diameter) scattered throughout it and also conspicuously associated with the fiber strands in the sclerotic-fiber hypodermal zone. The fiber strands are arranged in 2–3 alternating rows, the individual strands being somewhat radially elongated. A rather striking character of the species is the large "compound" resin canals running horizontally through the stem. They measure 1.3 mm. in diameter and are approximately six times the size of the vertical canals. Figure 18 illustrates several of these canals at the same magnification as the vertical canals in fig. 17. They are lined with numerous small triangular and diamond-shaped secretory cells which appear to contain the same black resin substance as the canal itself.

The leaf traces are given off from the narrow ends of the flattened steles and are initially quite large, consisting of 10–12 or more primary tracheids which divide farther out in the leaf bases into numerous smaller bundles. Three leaf bases are shown in fig. 16, two detaching themselves from the narrow transverse extremities of the stem and approximately parallel to it, while the third is being given off from the stem's broad side and at right angles to it. Thus it would appear that in *M. elongata* we are dealing with a creeping stem of possibly dorsi-ventral symmetry. As stated earlier, the dimensions of 6 × 1.5 cm. for the stem can be only slightly attributable to crushing while the equivalent asymmetry of the steles and general lack of any crushed tissue indicate the form to be more or less characteristic of the living plant. In addition, the 7 cm. of stem length of our specimen exhibits rather short internodes, with several leaf bases given off in the same bilateral plane from the narrow opposite stem sides.

The position of the stem on the edge of the containing coal ball prevented observation of more than the one dorsal leaf base shown in fig. 16. However, it seems plausible that these erect leaves were produced between internodes as short as the lateral ones.

As implied previously, M. *elongata* is most closely comparable to M. *distelica* on the basis of the extreme endocentric secondary growth. However, in the possession of three steles, which at no time show any tendency towards fusion, the difference in primary wood, fewer and uniseriate rays, and square secondary tracheids, as well as the large compound resin canals and apparent dorsi-ventral habit, M. *elongata* is clearly distinct and of specific importance.

The species name *elongata* is assigned in recognition of the asymmetric transverse elongation of the steles (10 × 2 mm.), as well as the equivalent transverse elongation of the stem as a whole.

Diagnosis:

Stem asymmetric to bilaterally symmetric, approximately 6 × 1.5 cm. in diameter, only slightly crushed in the smaller dimensions. Steles 3, extremely endocentric, 2 opposite one another in stem center, the third isolated to one side, retaining their relative positions and not fusing or dividing in over 7 cm. of stem length. Vertical resin canals numerous, averaging .2 cm. in diameter; fewer horizontal, large compound resin canals averaging 1.3 cm. in diameter. Habit creeping or climbing with leaves being given off from sides and dorsal surface of stem.

Locality: Atlas strip mine, Wilson County, Iowa.

Horizon: Pennsylvanian, Des Moines Series.

Type Specimen: Fig. 16. Slide 1617, in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Medullosa endocentrica, sp. nov.:

This third new medullosan stem comes from coal-ball material found in a stream bed outcropping near Berryville, Illinois. The location is near to that from which Steidtmann (1937) described M. *Noei,* and the horizon is the same, being determined as the upper part of the McLeansboro group of the Pennsylvanian of Illinois. The coal ball containing the specimen was 15 cm. long by 8 cm. wide. The stem followed a straight course through almost the complete longer axis, being itself 12 cm. long and 1.2 × .7 cm. in diameter. These dimensions are of the stelar system only, the cortex and other external tissues having been lost. However, as can be seen by referring to fig. 20, the unique appearance of the steles seems to justify recognizing the specimen as a new species and possible culmination of endocentric development, in spite of the lack of information as to the stem's external anatomy.

The stem consists of 3 steles, 2 of which are 5 × 5 mm. in diameter, the third, 2 × 1.5 mm. in diameter, situated on the side equidistant between them. Secondary growth is almost entirely endocentric, only one of the larger steles showing a very small amount of exocentric growth. These characters are constant for the entire 12 cm. of stem length as are also the relative stelar positions. Thus there can be little doubt that this extreme centripetal growth was a distinct feature of the living plant, and the evidence also suggests that the stelar system had achieved a degree of uniformity not found in any of the other Anglorota species.

The primary area of each stele is oval in transverse view, and measures 1.5 × 1 mm. in the 2 larger steles. It consists of scattered groups of large metaxylem cells intermixed with considerable conjunctive parenchyma. The protoxylem appears to consist of two small exarch groups of tracheids with annular thickening while the metaxylem shows the characteristic dense reticulate bordered pitting.

The secondary growth is produced in a fan-like pattern, radiating towards the stem center for an average of 15 cells in the large steles and 6 cells in the small stele. The transverse dimension of the cells increases gradually from the innermost to the outer rows but on the average is quite large, around .2 mm. The rays are of great height, more than 1.7 cm., and in the wood are uniseriate or at the most 2 cells wide. They commonly separate radial rows of 2–3 tracheids (fig. 22).

The pitting of the secondary wood is bordered and densely reticulate on the radial and oblique-tangential walls, with relatively few scattered pits on the directly tangential surfaces. The length of the individual tracheids is also quite extreme, an almost perfect tangential section showing them to be over 1.7 cm. Adjoining the outermost secondary wood (and continuous with it in general pattern and ray position) is a rather disorganized tissue which we were at first inclined to interpret as undifferentiated secondary wood. It consists of large thin-walled cells, similar in size and shape to the secondary tracheids but completely unpitted. On entering this zone the thin rays of the wood become greatly expanded, averaging from 4 to 8 or more cells in width, and appearing to be completely mature in their development (fig. 21). This point, along with the total absence of any rudimentary pitting, in either the tangential or radial walls of the vertical elements, in our opinion, makes it very unlikely that the cells are immature secondary tracheids. On the other hand, one or two of our tangential peels through this zone shows vestiges of what appear to be disarranged transverse walls with extremely small pores similar to the sieve plates of living plants (fig. 23). Scott, in his description of *M. anglica,* has pointed out that the rays become much wider in the phloem zone, while exceptionally large sieve tubes are common to plants of vine-like habit. Therefore, on the basis of the above evidence (which may be not entirely conclusive), along with the position of the tissue, we are inclined to consider it tentatively as phloem-like in nature.

Lying between this phloem region of the three steles is a thin parenchymatous zone of vertically elongated cells in which are scattered numerous resin canals containing their opaque resin rodlets. The entire stelar assembly is completely surrounded by a thin layer of dark, crushed cells of possible periderm nature.

The specific name *endocentrica* is assigned on the basis of the complete and constant centripetal secondary growth.

Diagnosis:

Steles small, not exceeding 5 × 5 mm., 2 opposite one another and of equal size, the third smaller, situated on the side between them. Secondary growth completely centripetal. Primary xylem exarch. Metaxylem with considerable conjunctive parenchyma. Rays 1–2 cells wide, expanding in the conspicuous phloem zone to 4–8 cells in width, exceeding 1.5 cm. in height.

Horizon: Upper part of the McLeansboro group, Pennsylvanian of Illinois.

Type: Fig. 20. Slide 1619 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Discussion:

As stated previously, *Medullosa endocentrica* appears to represent the ultimate in centripetal secondary development, and accordingly its closest affinities lie in the direction of *M. distelica* and *M. elongata.* It differs from the former primarily in possessing a third distinct small stele, constant for the whole stem and in the more perfect symmetry of the opposing "twin" steles. It differs from *M. elongata* in stele shape (*M. elongata* averaging 10 × 2 mm.), as well as in the character of the primary wood and amount of conjunctive parenchyma. *M. endocentrica* differs from all the other Medullosas in its constant degree of endocentricity and the possession of a unique phloem zone of exceptionally large sieve tubes.

It is possibly significant that here, as in *M. elongata,* we appear to be dealing with a stem of more bilateral (dorsi-ventral) than radial symmetry. From the form of stele development in *M. endocentrica* (fig. 20) leaf traces could only have been given off in the three planes opposite the abaxial sides of the primary xylem groups. Thus while the orientation of the steles is somewhat different in the two species it is likely that the phyllotaxy was similar, the leaves being produced laterally and vertically (dorsally) with the side lacking a leaf trace source being considered ventral.[1] The predominance of 3 stele forms in the Medullosae is perhaps indicative of this trend, which, however, reaches its inescapable climax only in the extremely endocentric species. *M. endocentrica* has apparently almost reached the limit of its potential stem enlargement through secondary growth but it is still much too small to permit interpretation as an arborescent plant. Therefore it could not possibly

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[1] It should be pointed out here that since the traces show no evidence of "girdling," the direction of their initial departure is a valid indication of the stem's phyllotaxy.

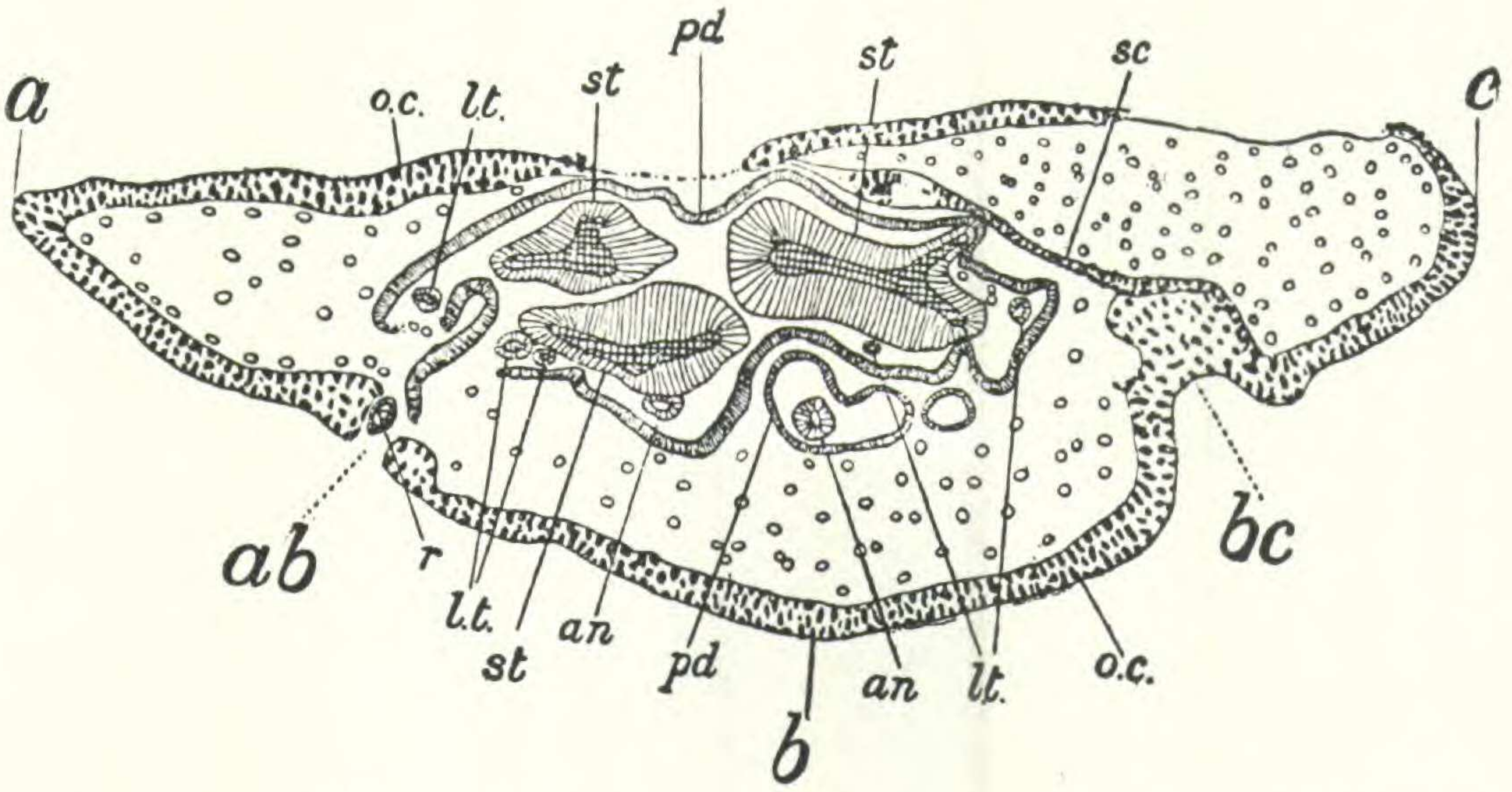
have attained a habit comparable to that suggested in the reconstruction of *M. Thompsonii* (Andrews, 1945). Also if it produced relatively large *Alethopteris*-type fronds, as appears likely from the numerous associated leaves, it must have been a prostrate or climbing vine since the small stem would be incapable of supporting any such great weight. Thus the line of endocentric development from *M. distelica* and *M. elongata* to *M. endocentrica* appears to be one leading to constantly diminishing size accompanied by a change from radial symmetry of the stem with complete spiral phyllotaxy to a bilateral, dorsiventral symmetry with lateral and dorsal leaves. Extreme asymmetry can accordingly be seen to be an advanced rather than primitive character, which as it reached its climax resulted in a line of "dead-end" development in which the stem size was small and fixed. In this viewpoint we agree with Schopf (1939, page 204) where he states:

> It seems more tenable to consider the distelar condition in the new Nashville *Medullosa* as reduced from a more polystelar type rather than as directly derived from an ancestry reminiscent of *Sutcliffia*. It is also apparent that the extreme endocentric asymmetry found in *M. distelica* is not a primitive feature.

We have included in the above quotation Dr. Schopf's statement on a distelar condition probably resulting from the fusion of a polystelar type in that it also agrees with our conception of what seems to be another and more important line of development in the Medullosas. As pointed out in the discussion of *M. primaeva*, a polystelar condition with numerous small radially symmetrical steles would seem to have arisen most logically by stelar proliferation of a monostelic stem with a similar small symmetrical stele. Then through subsequent tendencies to stelar fusion the line would lead through the small tetra- and tri-stelar forms to the large asymmetric stelar forms such as *M. anglica* and *M. Noei.*

The fact that the smallest species *(M. primaeva* and *M. pusilla)* have the most radially symmetrical steles while the larger species *(M. Thompsonii, M. elongata, M. distelica* and *M. anglica)* all have greatly elongated (transversely) asymmetric steles is evidence, in our opinion, that the latter have been derived from polystelic fusion. (A good example of this point is illustrated in Andrews' (1945) diagrams of stelar fusion in *M. Thompsonii* where it can be seen that the fusion produces a larger, more asymmetric and more endocentric stele). Where the fusion standardized itself at 3 steles of approximately equal size, or with one slightly smaller, a balance appears to have been reached which was only upset by the origin of the erratic cambial growths of *M. Noei.*

Regarding the phyllotaxy of the predominately 3-steled forms it may also be pointed out that while the leaf arrangement has been mainly interpreted as spiral, Scott, in working with a specimen of *M. anglica* one foot in length, showed that the leaves were still produced on only three sides of the stem (text-fig. 1). While Scott himself did not enlarge on this evidence, it seems to imply (when correlated with forms such as *M. elongata* and *M. endocentrica*) that the significance of the normal number of 3 steles in the Carboniferous Medullosas lies in the essentially dorsi-ventral habit of the plant as a whole. As may be noted in text-fig. 1 of *M. anglica* (which is typical for most of the 3-stele species), the steles are arranged in the shape of a flattened triangle, the obtuse apex being always towards the flattened side of the stem from which the dorsal leaf bases are produced, while the steles at the opposite acute angles are oriented towards the position of the lateral leaves.



Text-fig. 1. *Medullosa anglica:* *o.c.*, outer cortex; *l.t.*, leaf trace; *st*, stele; *pd*, periderm; *sc*, sclerotic strands separating petiole from stem; *r*, root; *an*, accessory strand. *A, B, C, AB* and *BC* represent the points of leaf departure with the phyllotaxy being 2/5. *Note that this arrangement still leaves one side of the stem completely devoid of leaves; so that the habit may be assumed to have been dorsi-ventral* (after Scott).

This bilateral symmetry is borne out also in the over-all stem shape of nearly all of the 3- to 4-steled group. *M. centrofilis* had a stem diameter of 5 × 1.5 cm.; *M. pusilla*, 2.2 × 1.3 cm. (Scott points out that the larger diameter here had lost considerable tissue and was probably still greater in life); *M. Thompsonii*, 7 × 2.5 cm.; *M. anglica*, 10.5 × 3.7 cm.; *M. elongata*, 6 × 1.5 cm. *M. endocentrica* also undoubtedly had a flattened stem but the lack of preservation of the outer tissues in our specimen precludes such measurements. All of the above figures include the attached leaf bases, but since it has been shown that these were always decurrent for long distances on the stem and more or less overlapped, the measurements give a truer habit proportion than those of the stem alone would. The asymmetry can be seen to be quite constant in a proportion of 3:1, which fact alone makes it extremely doubtful that it is altogether due to crushing. De Fraine states for *M. centrofilis* that "the shape of the stem with its covering of leaf bases was thus distinctly flattened."

It would seem that the dorsi-ventral habit, while most obvious in species such as *M. elongata* and *M. endocentrica* was also the rule in the majority of the other species. *M. Thompsonii* is a possible exception since rather careful study of the type specimen seems to indicate that in this particular stem the orientation of the stelar assembly tends to vary, so that the planes of leaf trace departure are distributed more generally in the four opposing radii and thus supply petioles in a true radially symmetrical spiral phyllotaxy. However, such variations are not too unusual. *Selaginella,* for example, in the two present-day species, *S. rupestris* and *S. apoda,* shows a variation from erect plants with radial symmetry to creeping plants with bilateral symmetry. This view, accordingly, makes it necessary to visualize the Medullosae as primarily an assemblage of creeping or climbing plants rather than as comparable to present-day tree ferns. The prostrate habit has previously been postulated by several earlier workers on the basis of the small stem of the Anglorota plants, while the great stem length recorded by Weber and Sterzel (1896) for some of the Permian specimens is almost conclusive proof of the vine-like habit of the much younger species. Weber and Sterzel state:

> Bei Stämmchen wie M 43, das bei 92 cm. Länge nur einen Durchmesser von durchschnittlich 8,8:4.4 cm. besitzt, könnte man wohl an die von Göppert & Stenzel vermutete Schlingpflanzennatur der Medullosen denken. . . . Die im Anhang sub 1 Seite 105 (64) geschilderten Medullosenstämmchen beweisen dass insbesondere *Medullosa stellata* einé schlank-cylindrische Gestalt mit periodischen Anschwellungen des Holzkörpers und auch im Uebrigen merklich wechselndem Durchmesser haben könnte, so das man, wie schon erwähnt, mit Göppert & Stenzel an Schlingpflanzen denken könnte. In dieser Form des Wachstums liegt wohl auch das verhaltnismässig häufige Vorkommen von Bruchstücken dieser Art begründet.

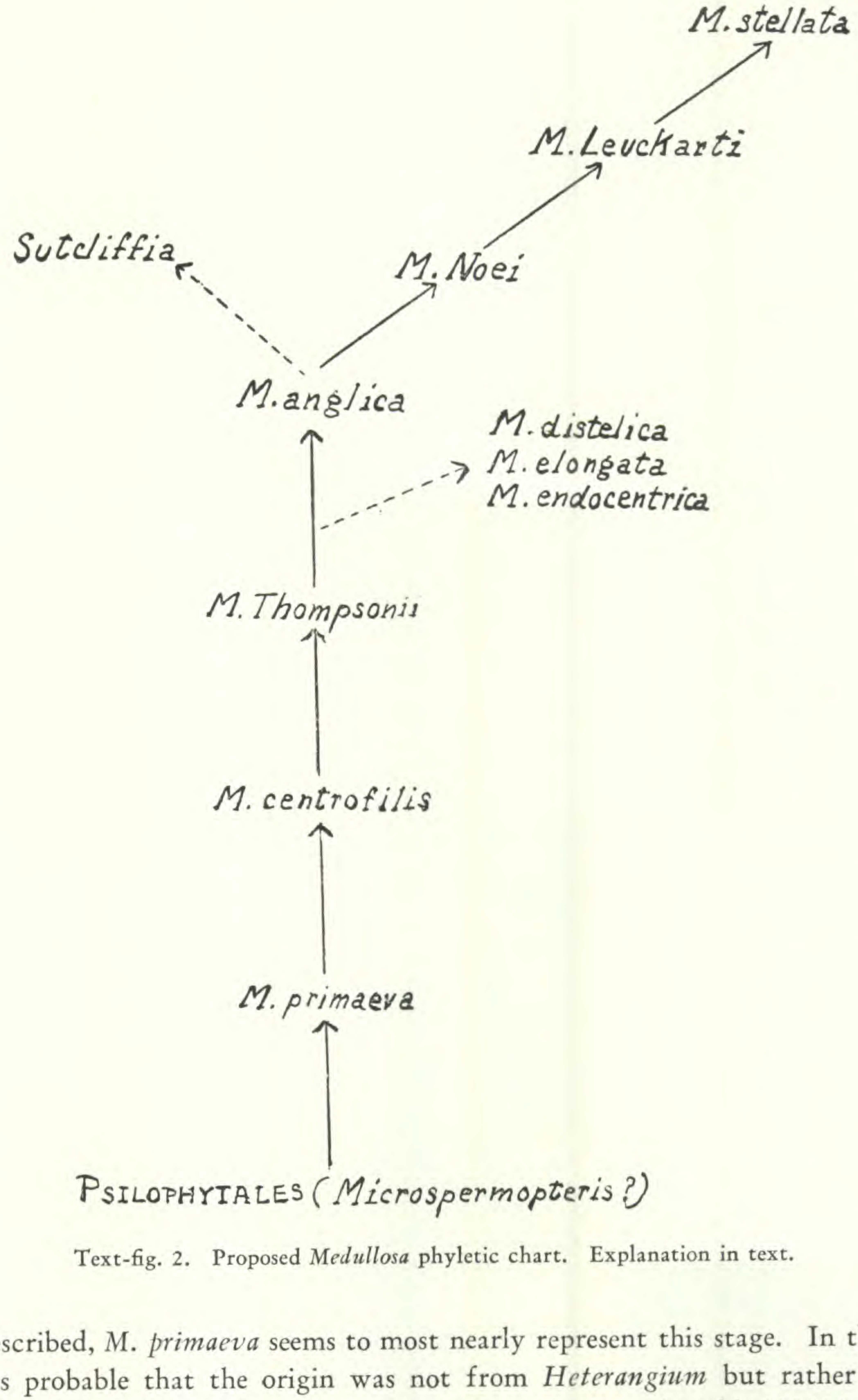
In addition to the evidence offered by the dorsi-ventral flattened stem, the phyllotaxy, and the great stem length in relation to its width, there is also considerable anatomical proof that the Medullosae were primarily prostrate or climbing vines. Solereder (1908) has shown that unequal xylem growth and flattened stems are characteristic of many living lianas, while Westermaier and Ambronn (1881) have pointed out that tracheids and sieve tubes of more than average diameter are typical of living climbing plants. As noted by Andrews (1940), the tracheids of *M. Noei* and *M. anglica* may reach a diameter of 250 μ (larger than most vessels) while *M. endocentrica* has extremely broad sieve tubes.

Although the acquisition of concentric rings of exocentric secondary wood permitted an increase in size of the Permian Medullosas, along with a possible return to a radially symmetrical spiral phyllotaxy, the vine-like habit of their Carboniferous predecessors appears to have been largely retained.

The absence of a vine-like habit in the living or fossil cycads need not present any insurmountable difficulties in retaining the theories of their origin from the Medullosas, since, with the increased girth afforded by centrifugal secondary growth, the developmental trend may be assumed to have been away from climbing towards arborescent forms. This change may also have been influenced and accompanied by a disappearance from the scene of the potentially supporting *Psaronius, Calamites* and *Lepidodendron* through a gradual shift to a xerophytic environment.

To summarize and restate our evidence:

1. A large number of small symmetrical steles with almost solid primary wood represents the primitive condition. Of the different specimens which have so far



Text-fig. 2. Proposed *Medullosa* phyletic chart. Explanation in text.

been described, *M. primaeva* seems to most nearly represent this stage. In this light it seems probable that the origin was not from *Heterangium* but rather from a more ancient form possibly akin to *Microspermopteris*. Arnold (1940) has described a small polystelic stem from the Middle Devonian of New York to which he has given the name *Xenocladia medullosina*. It consists of 9–10 small (not much over 1 mm.) steles with a small solid protostele. He states that: "*Xenocladia* may eventually prove to be a representative of some intermediate stage between the Psilophytales and certain of the polystelic Pteridosperms." While we are not inclined to attach too much weight to any direct connection between *Xenocladia* and a stem such as *M. primaeva,* it does show the possible origin of a polystelic structure contemporaneous with *Rhynia* and *Hornea* and, along with *Microspermopteris,* indicates a psilophytalian origin for the pteridosperms.

2. Through subsequent tendencies to fusion the stele number eventually became standardized at 3, with occasional variations of 2 or 4 through further fusion or division.

3. Accompanying the above transition there was an increase in the size of the plants and consequently of the leaves, which (since in a closely grouped polystele the leaf traces of necessity are produced from the abaxial sides) tended to inhibit exocentric (centrifugal) secondary growth and thus resulted in an endocentric (centripetal) asymmetry of the steles.

4. As this endocentricity became pronounced the production of leaf traces also became more localized on the abaxial stelar sides, resulting in a phyllotaxy of lateral and dorsal leaves (text-fig. 1, *M. anglica*). *M. elongata* and *M. endocentrica* represent a climax of this trend which in the latter undoubtedly formed an end development.

5. Where the endocentricity did not reach such extremes, the plants tended to increase in size through the production of accessory vascular strands *(M. anglica),* while eventually tangential secondary growth (to compensate for the limitations of endocentric growth), along with the origin of prolific erratic cambial zones *(M. Noei),* led to the larger and more complex Permian species. Text-fig. 2 shows a provisional and tentative phyletic chart based on the above points. Although the horizon of all of the American species is considerably higher than that of the European ones, the evidence of the stems themselves still seems to justify the reverse grouping. For the reasons given above *M. primaeva* constitutes the base with the main line of development leading through *M. Noei* and *M. Leuckarti* to the Permian forms, while the three extremely endocentric species constitute a dead-end side chain of development.

Medullosa anglica is placed near the top because of its relatively large size and erratic "periderm" resembling that of *M. Noei.* The large leaf traces with secondary growth may be viewed as advanced and of the nature of specialized accessory vascular strands to supply the increased needs of the enlarged petioles. Also *Sutcliffia,* differing from *M. anglica* primarily only in its monostelic structure, may be regarded as resulting from a fusion of the three steles.

Medullosa Noei Steidtmann:

Steidtmann (1937, 1944) established *M. Noei* as the first clearly recognizable American species of the genus and gave us an excellent description of the salient features and peculiarities of the stem as well as the associated leaves, roots, and seeds. However, the holotype on which he based most of his description had only one stele with portions of two others, while our present specimen consists of a nearly entire stem with three large complete steles. It was collected from the same outcrop near Berryville, Illinois, that produced M. *endocentrica* and is exceptionally well preserved in its cellular details. The coal ball, of which the stem constituted almost the entire bulk, was 28.6 cm. long and approximately 16 × 7 cm. wide in the middle portion, tapering to blunt points at either end.

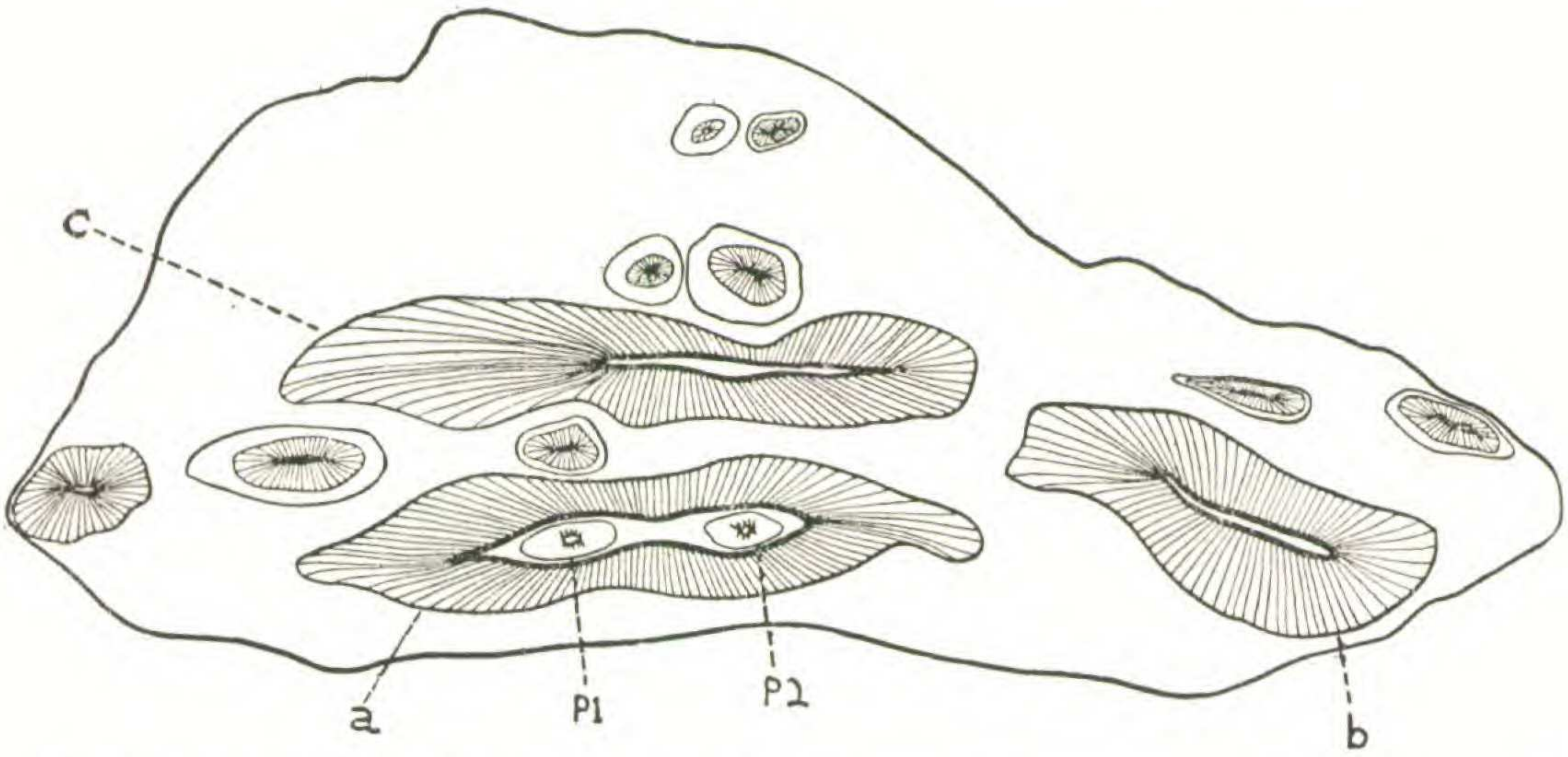
The essential features offering possibilities of an enlarged interpretation and understanding of the species are:

1. The presence of a distinctive phloem zone characterized by broadened extensions of the medullary rays.

2. "Periderm rings" which show a transitional development of secondary wood, a stelar origin, and a remarkable similarity to the Permian Medullosae "star-rings."

3. Adventious roots, which run for long distances through the cortex parallel to the steles, range from triarch to pentarch, and show a well-preserved aerenchymatous cortex.

Before discussing these points in detail a brief description of the stem as a whole will be given. As shown in text-fig. 3, there are three large steles, tangentially elongated, which occupy the major portion of the area as seen in transverse section. Throughout the 28.6 cm. of stem length they remain essentially independent although steles *a* and *c* occasionally partially fuse and then re-separate. Their orientation with relation to one another is similar to that of the steles in M. *elongata,* two of the steles being side by side while the third occupies a position off to one side. They average 6 × 1.5 cm. in diameter and show no particular endocentricity, the secondary growth being the greatest in a tangential plane rather than towards the stem center. This is a greater elongation than was usual in Steidtmann's specimen, although he records that the stele did at times reach a measurement of 6 × 1.8 cm., which is certainly close to the above. For the rest, the primary and secondary wood are essentially equivalent to Steidtmann's specimen and exhibit primary tracheal bundles, prolific and erratic "periderm" growths, and tetrarch roots originating in and running through the primary area. The cortex is crowded with "periderm" rings and tangentially elongated bands, as well as with the numerous large adventitious roots with their many small branches. The hypodermal sclerotic zone is present as the outermost limiting tissue, the leaf bases being absent. While there are apparent general differences between the present specimen and Steidtmann's diagnosis of M. *Noei* (mainly in the lack of any pronounced endocentric growth, and absence of a definite broad periderm zone), it is felt that the variations fall within those allowable to a species, particularly in the Medullosas. The following descriptions of the previously outlined characters are therefore intended solely as an addition to the M. *Noei* diagnosis and not as of new specific or varietal importance.



Text-fig. 3. *Medullosa Noei: a, b,* and *c* indicate the three steles. *P1* and *P2* are the "periderm" or "cambial" rings. All of the other vascular strands represent adventitious cortical roots. Additional explanation in the text. × 4/5.

It is understandable how a great deal of the *M. Noei* material might be examined without observing the striking phloem rays, since they are only occasionally evident even in the exceptionally well-preserved present specimen, their place being usually occupied by invasions of the prolific "periderm" tissue. However, as shown in fig. 26 the rays with their dark brown secretory cells sometimes form a quite prominent fringe around the stele. They vary from 1 to 2 mm. in length (outside the wood) and from 4 to 8 cells in width, spreading out fan-like towards their outer margin. The cells are radially elongated and contain numerous black globules of evident secretory nature. The tissue lying between the rays is seldom well preserved. Whatever sieve tubes that might have once existed are consistently represented by disorganized cellular fragments. The general aspect as seen in transverse section is rather similar to the expanded "phloem rays" of *M. endocentrica,* the rays in both species being characterized by their dark brown color and black secretory cells, as well as in their greater width as compared to their structure in the xylem.

As mentioned previously, numerous adventitious roots run through the cortex. They vary from tetrarch ones, which apparently originate in and run through the primary part of the stele for some distance before emerging, to triarch and pentarch ones, which seem to arise in the "periderm" adjoining the stele and follow a vertical course through the cortex for long distances before emerging. Some of these cortical roots attain considerable size (up to 2 × 2.5 cm.) and are sometimes difficult to distinguish from small steles (text-fig. 3). They are often beautifully preserved and show an aerenchymatous cortex, a feature strongly suggestive of a moist or aquatic habitat (fig. 25).

It may be pointed out here that Worsdell (1906) has found that the Cycadaceae show a similar variability in root anatomy with pentarch or tetrarch roots normally borne adventitiously near the base of the plant and the diarch and triarch roots produced towards the apex.

In Steidtmann's (1937) preliminary report he stated that M. *Noei* apparently had three large steles with at least two "star rings." Later, in his more intensive and complete treatment of the species (1944), he indicated that the structures which he had initially reported as "star rings" proved on closer observation to be "large concentric strands of the ever-present periderm." Now, our present specimen seems to show that Steidtmann's first view was the correct one and that the periderm or "cambial" rings possibly do represent developing "star rings."

De Fraine (1914) points out that the "star ring" of *M. centrofilis* differed from the star rings of the Permian stems in that it was basically protostelic while the latter, as implied by the constant reference to a "partialmark," were largely parenchymatous. This distinction is shown in pl. 10, where not only the difference between the *M. centrofilis* type of "star ring" and that of *M. stellata* is evident but also the considerable similarity between the latter and an M. *Noei* "cambial ring." Accordingly, the use of the term "star ring" for the fourth small stele in *M. centrofilis* was probably ill-advised, as it obviously had little in common with the majority of the structures so named in the Permian species but merely constituted a small independent stele. On the other hand, the evidence seems clear that in M. *Noei* we have, for the first time in a Carboniferous stem, the appearance of structures equivalent to the Permian "star rings." The fact that it was not until after a careful examination of his specimen that Steidtmann decided the structures were too similar to the profuse erratic periderm growths to be called "star rings" suggests that the "sternringen" of the poorly preserved, silicified stems of "des Rotliegenden von Chemnitz-Hilbersdorf" may also have been "periderm growths." Certainly the observable detail of the Weber & Sterzel specimens was hardly comparable to that to be found in good coal-ball material.

Steidtmann (1944) discussed the advisability of using the term "periderm" for these prolific growths, and came to the conclusion that it was valid since it did not necessarily imply suberization. However, in our specimen it can be seen that the tissue (at least that which forms many of the rings) originates in the primary part of the stele, and, instead of being an invasion from the cortex, itself produces outgrowths which occasionally penetrate the secondary wood and extrude into and through the cortex. Figure 24 shows a ring from the primary area of stele *a* (text-fig. 3) in which a certain amount of differentiation into secondary xylem has taken place, indicating that the tissue was more of a true cambial nature than periderm. That these "cambial rings," like some of the roots, originated within the stele is clearly shown by their continuous vertical course throughout the stele both above and below the occasional cortical invasions.

There is also the new evidence which has come to light in M. *Thompsonii* that the "star rings" may, in part, be derived from a *congestion* of leaf traces. Figure 59 shows a diagram of a portion of M. *Thompsonii* which has just given off a petiole. The hypodermal fiber strands are lacking on the one side and the cortical area containing the outgoing traces is considerably diminished. Arranged in a line along the stem margin in this area are numerous thin-walled xylem "rings" with a central core and radial secondary tissues (figs. 30 and 59). Successive peels, downward through the stem, show that these "rings" result from a fusion of two or more outgoing traces. It seems that the traces, while still being prolifically formed, lacked an expanding cortical area in which to scatter out, and consequently became congested and fused with a subsequent production of secondary growth. The limitations of the M. *Thompsonii* material do not allow observation of the final disposition of these "rings," but it seems likely, with the increase in the cortical area on approaching the next node, that the "rings" or "aggregate" traces may have redivided and lost their secondary wood.

If in the early ontogeny of the Permian Medullosas there were numerous leaf traces produced towards the center of the stem, the same congestion and fusion might possibly have resulted in the medullary "star rings" of M. *Solmsii,* with the central position inhibiting subsequent redivision. We are inclined to follow Worsdell (1906) rather than De Fraine (1912) in that (as pointed out in the previous discussion) we regard the Permian Medullosas as leading to the Cycads, with *Sutcliffia* as an advanced rather than primitive member of the Medullosae. The above theory of a leaf trace origin for the "star rings" would offer further evidence for Worsdell's view that the collateral rings of the Permian Medullosas and the Cycads are "composed of the one-sided remnants of a number of steles," since only in such a polystelar structure could the leaf traces be produced towards the center.

To pursue the conception still further, De Fraine (1912) states: "There appears to be no serious objection to the view that the 'meristeles' of *Sutcliffia* are homologous with the leaf trace strands which leave the stele in M. *anglica* for both appear to be entirely used up in the formation of foliar bundles." Following the same reasoning, the marginal vascular rings in M. *Thompsonii* may also be considered as homologous to the above in that they differ only in forming in the cortex rather than at the stele margin, while the Permian "star rings" may also be homologous except that they were not used up in the formation of foliar bundles due to their internal position. Thus the extra-fascicular zones and accessory cortical and pith strands (star rings) of *Medullosa, Sutcliffia,* and the present-day Cycads are possibly all equivalent in that they may represent aggregations of fused leaf traces around which the secondary growth has become concentric producing rings or (where adjoining groups become contiguous) forming collateral bands.

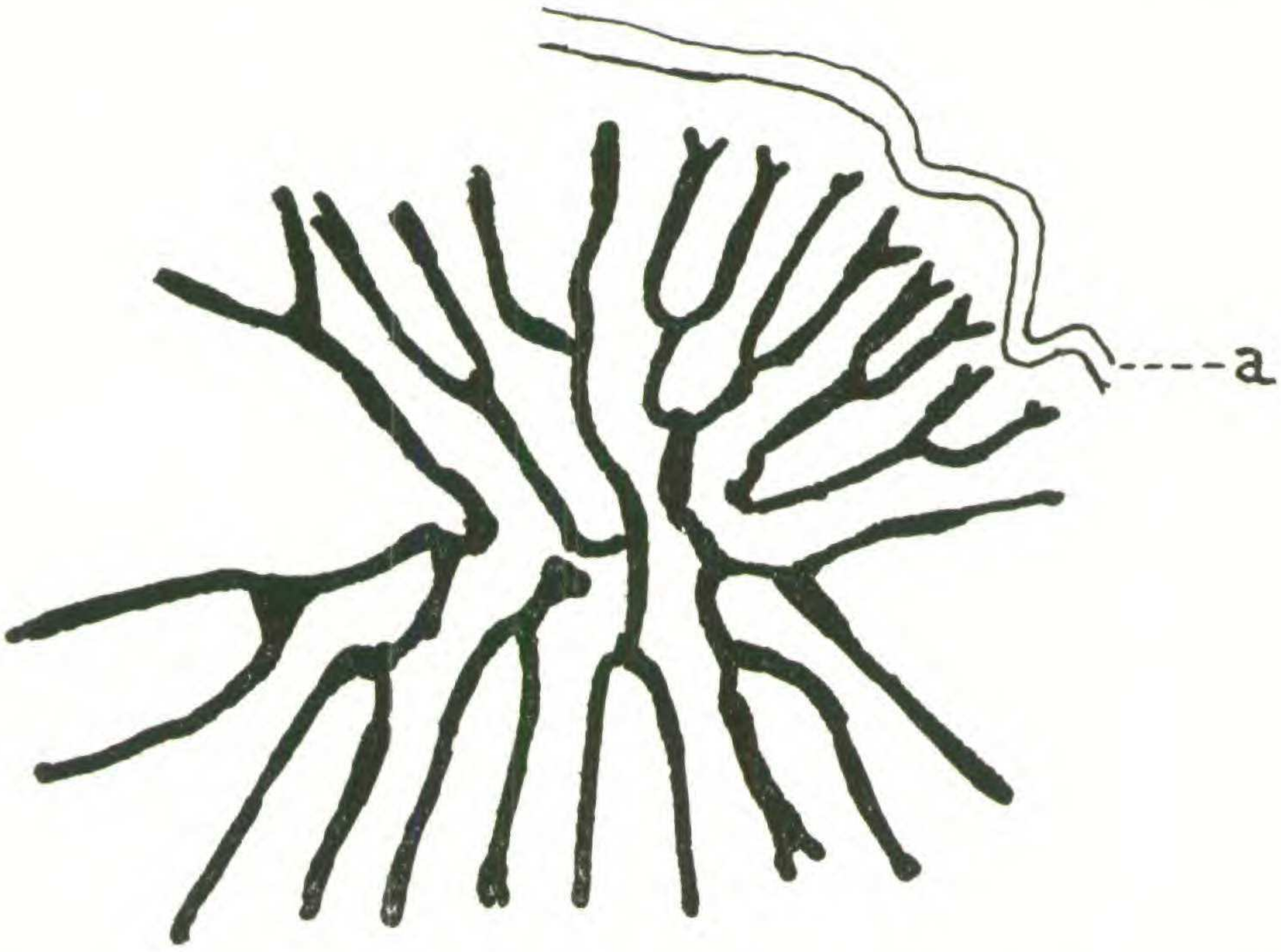
SOME MICROSPORANGIATE FRUCTIFICATIONS ASSIGNED TO THE MEDULLOSAE

The abundance and variety of *Medullosa* stem and petiole remains in the Iowa and Illinois coal balls indicate clearly that the group was a dominant and widespread feature of the Carboniferous flora. As Andrews (1948) points out: "The wide range in anatomy exhibited by the Upper Carboniferous and Permian medullosas almost certainly represents an assemblage of familial or possibly ordinal rank rather than simply a genus." Accordingly, it is not surprising to find a corresponding diversity beginning to be evidenced among the other organ genera usually associated with and regarded as belonging to the *Medullosa* stems. This is particularly true of the interesting microsporangiate fructification known as *Dolerotheca*. *Dolerotheca* is characterized by a large campanulum containing radially arranged rows of paired tubular sporangia. The evidence for its being a medullosan pollen-bearing organ is almost conclusive although it has not as yet been found attached. Dr. J. M. Schopf (1948), in addition to describing three new species from Illinois coal balls, has given a comprehensive historical, taxonomic, and phylogenetic discussion of the genus and certain allied forms. Therefore we shall limit ourselves here to describing briefly two additional new species of *Dolerotheca* from coal-ball material collected at the What Cheer Clay Products Co. coal mine, What Cheer, Iowa. This horizon is designated only as the Des Moines Series, Pennsylvanian, but as we shall point out later may be tentatively assumed to be of considerably greater age than the lowest Illinois horizon in which petrifactions of *Dolerotheca* have been found.

Dolerotheca sclerotica, sp. nov.:

The general shape is that of a broad rather shallow campanulum approximately 25 mm. in diameter and 5–7 mm. deep (fig. 45). The epidermis of the proximal sides is represented by a layer of tangentially elongated cells with conspicuous dark contents, on which are scattered a few very small capitate glandular hairs (fig. 58). Just within this layer is a definite sclerotic hypodermal zone, .4 mm. in thickness, of empty isodiametric cells, only approximately 1 out of 30 showing a black secretory plug (fig. 49). Lying immediately inside this latter zone is the parenchymatous ground tissue of the fructification which, as in the Illinois species, seems to enclose and "constitute the walls of the sporangia." It forms a network of uniform thickness, 2–3 cells, composed of thin collapsed parenchyma in which are numerous large secretory canals with their dark, opaque contents.

The double radial rows of tubular sporangia are separated by very conspicuous sclerotic bands, 4–6 cells thick, which are normally interrupted at the junction with the alternating lysigenous tubes but may occasionally form almost continuous radial septa from the center of the fructification out to the marginal ground tissue. The individual sclerotic fibers are small, 50 μ in diameter and up to 500 μ in length. The bands bifurcate from 1 to 3 times, the first time about ¼ the distance from the center, the second at about half the distance from the center,



Text-fig. 4. *Dolerotheca sclerotica:* Diagram showing pattern of bifurcations of sclerotic-fibrous framework. *a,* campanulum wall. Explanation in the text. × 4.

and the third time within 1 mm. or less of the marginal peripheral ground tissue (text-fig. 4). Additional paired rows of sporangia are intercalated at the inner bifurcations while the marginal division is generally too near the periphery to allow space for more than the insertion of a single sporangium. The lysigenous tubes are much less conspicuous than in the three Illinois species. In the latter the tubes are enclosed by walls 3–6 cells thick, having circular to oval locules, while the equivalent structures in *D. sclerotica* are represented merely by rectangular spaces between the thin (1 cell) tangential walls of adjoining sporangia (figs. 48 and 50). As in *D. formosa* Schopf, the vascular bundles of our specimen "are noteworthy for their obscurity." They consist of 3–4 small annular tracheids apparently restricted to the marginal area of the campanulum. The bundles lie in the secretory parenchymatous tissue which alternates radially with the sclerotic bands, there usually being but one bundle in each radial strand 1 mm. within the hypodermal zone.

D. sclerotica appears to have had considerably less dehiscence tissue than the Illinois species, although the distinction is possibly doubtful since our specimen was poorly preserved at the distal end. However, as shown in fig. 48, the groundwork of the fructification consists solely of the fibrous sclerenchyma bands with a parenchymatous network of secretory cells, and it is only at the extreme periphery that fragments of tissue of possible dehiscent nature are found. The sporangia average 500 × 700 μ in diameter, only the centermost being vertical. The outer sporangia originate on the ascending inner slope of the campanulum and tend to follow the general shape, curving outward and upward (fig. 45). The spores are unusually large averaging 470 × 200 μ, in the longer dimension exceeding that of all of the Illinois species. They are marked by a monolete suture similar to that described for *D. formosa.*

The major distinctions between *D. sclerotica* and the three Illinois species—*D. villosa, D. Reedana* and *D. formosa*—are as follows:

1. Few very small capitate epidermal hairs as compared to the relatively dense pubescence of the other three species.
2. A homogeneous sclerotic hypodermal zone.
3. Lysigenous tubes which are merely gaps between thin-walled sporangia.
4. A dominating radiating framework of bifurcating fibrous sclerenchyma bands.
5. A greater amount of secretory cells in the parenchymatous ground tissue.
6. Larger prepollen or spores.

The differences may be said to be almost of generic importance and scope and lend further weight to the viewpoint voiced earlier that the Medullosae are probably a more heterogeneous group than can much longer be contained in a single genus.

Diagnosis:

A flattened campanulum up to 25 mm. in diameter. Epidermis of dark secretory cells, practically glabrous, with only a few capitate hairs. A conspicuous hypodermal zone of isodiametric sclerenchyma cells. Groundwork composed of radiating, bifurcating bands of fibrous-sclerenchyma enclosing a parenchymatous secretory tissue which composes the sporangial walls. Lysigenous tubes consisting solely of gaps between thin tangential sporangial walls.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 45. Slide 1628, in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Dolerotheca Schopfii, sp. nov.:

This species, like *D. sclerotica,* is based on a single specimen also from the What Cheer coal mine near the town of What Cheer, Iowa. The fructification had evidently been broken into fragments prior to fossilization since, although cellular preservation is excellent, only an estimated one fourth or less of the campanulum was present in the coal ball. However, from the individual sporangia (up to .6 × 1.3 mm. in diameter and their incomplete length of 15 mm.) it is possible to assume that the complete structure was comparable in size to *D. formosa* and possibly more tubular due to its apparent greater depth (figs. 51 and 53). Thus, it is considerably larger than *D. sclerotica.* Unlike the latter species also, its proximal surface is covered with an extremely dense pubescence of glandular hairs up to 5–6 cells in length. The cells are flattened, 3–4 times as broad as long, the terminal cell being slightly tapered. All the cells contain black opaque secretory masses (fig. 57). In the solid density of the hairs *D. Schopfii* is comparable to *D. villosa* but the gross appearance is closer to *D. formosa.*

Immediately within the hirsute epidermis is a broad (up to 1.5 mm. thick) hypodermal zone of large secretory canals (200 μ in diameter) scattered profusely throughout a homogeneous matrix of small fibrous sclerenchyma cells which average 50 μ in diameter to 500 μ in length. This zone is identical to and continuous with the ground tissue making up the tangential and central radial walls of the paired sporangia (figs. 46 and 47). The radiating framework of fibrous, sclerotic bands is not quite as prominent as in *D. sclerotica* but is still much more extensive than in any of Schopf's Illinois species. As in *D. sclerotica,* the radial bands are occasionally continuous for a space of 2–3 sporangia, although the more usual condition seems for the bands to have been interrupted at the point where they join the sporangial tangential walls (fig. 51). The individual fibers are approximately equal in size to those of *D. sclerotica.*

Probably the most distinctive character of the species is the apparent lack of lysigenous tubes which in the other species alternate radially with the tubular sporangia. While the fragmentary condition of the type specimen shows only a marginal portion of the original campanulum to a depth of about 6 sporangia, it can be clearly seen that the radially adjoining sporangia are separated only by a common wall of the secretory and sclerotic ground tissue (figs. 46 and 51). It is, of course, possible that this could represent an immature stage in which the cellular disintegration forming the lysigenous tubes had not yet taken place. However, the size of the fructification, which must represent considerable maturity, along with the apparent complete dehiscence of the spores, makes it seem much more likely that the lysigenous tubes were simply not developed in this species.

The vascular bundles are even more obscure than in *D. sclerotica.* They consist of only 1–2 annular tracheids and occupy a similar marginal position in the radial ground tissue just within the broad hypodermal zone.

As in *D. sclerotica,* there is no observable dehiscence tissue, which again may possibly be due to lack of sections through the distal end. Dehiscence had evidently been complete, and no spores were found in any of the sporangia.

In comparison with *D. sclerotica* and the three Illinois species the following characters of *D. Schopfii* are held to be of specific importance.

1. Absence of lysigenous tubes.

2. The broad secretory and sclerotic hypodermal zone continuous with and identical to the groundwork making up the sporangial walls.

3. The more tubular shape of the campanulum.

While the nearly glabrous stony outer tissues of *D. sclerotica* contrast strongly with the dense glandular hairs and thick secretory zone of *D. Schopfii,* the thick radial sclerotic framework in both, along with inconspicuous lysigenous tubes in *D. sclerotica* and complete lack of them in *D. Schopfii,* seems to show that the two species are much more closely related to each other than to the Illinois species.

The species is named in honor of Dr. James M. Schopf in recognition of his noteworthy work on the genus.

Diagnosis:

Campanulum an estimated 35 mm. in diameter and 15 mm. or more in depth. Proximal epidermis with a dense pubescence of broad glandular hairs; a broad hypodermal zone of large secretory canals in a homogeneous matrix of small fibrous sclerenchyma which is continuous with and identical to the groundwork forming the sporangial walls. Lysigenous tubes lacking, adjoining sporangia having a common tangential wall.

Horizon: Des Moines Series, Pennsylvanian.

Type: Fig. 51. Slide 1629 in the paleobotanical collections of the Henry Shaw School of Botany of Washington University.

Discussion:—

While accurate geological correlation of the horizon of the Des Moines Series producing these and other petrifactions described in this paper is still needed, the evidence of the fossils themselves would tend to indicate a position in the lower part of the series and possibly considerably older than the Carbondale of Illinois. This viewpoint is based on the following facts: Over a period of three years of investigating hundreds of coal balls from Illinois and Iowa (i.e., the Des Moines Series) what appear to be the more primitive plants are all from the latter horizon. *Microspermopteris aphyllum* (described earlier in this paper), with its very primitive habit and psilophytalian characters, is from the Des Moines Series; also *Medullosa primaeva* and *M. Thompsonii,* both of which have been tentatively placed at the bottom of the phylogenetic chart (text-fig. 2) as representing the most primitive stages of the known species. *Dolerotheca sclerotica* and *D. Schopfii,* with their large amount of sclerotic tissue, seem closest to *D. Reedana* which, in being from the Carbondale of Illinois, is the oldest of Schopf's three species. In addition, *D. sclerotica* and *D. Schopfii,* with their much more extreme sclerotic condition, apparent lack of dehiscence tissue, simple lysigenous tubes or complete absence of them, and larger prepollen size (in *D. sclerotica*), seem to indicate an evolutionary stage considerably below that of *D. Reedana.*

Since the much younger *Dolerotheca formosa* shows only isolated groups of sclerenchyma and *D. villosa* appears to lack them completely, the primitive state would seem to have been the almost complete radial septation (of a single telome?) by bands of fibrous sclerenchyma between which were borne the essentially independent radial rows of paired sporangia. If any other proof were necessary to show the radial rather than cyclic arrangement of the sporangia in *Dolerotheca* (Schopf, 1948) it is amply supplied in *D. sclerotica* with its almost continuous radiating network of fibrous-sclerotic bands. In addition, the more numerous and regular bifurcations of the radial framework and the nearly symmetrical intercalation of additional paired rows of sporangia seem indicative of a centrifugal direction of development.

Found in close association with *D. Schopfii* was the *Myleoxylon* fragment shown in fig. 54. A longitudinal section through its outer margin, in fact, shows the base of the fructification with its tissues apparently continuous with those of the petiole (fig. 52). While the continuity of tissues is not so complete as to allow a definite statement as to their connection, the association is extremely close and felt to be worth illustration and mention. If this condition does represent a true attachment it would seem to show that, unlike *D. Reedana, D. Schopfii* was sessile and attached directly to fairly large divisions of the rachis.

SUMMARY

1. The known Carboniferous flora is outlined and it is suggested that it falls into large tree-like, microphyllous groups and small shrubby or climbing megaphyllous groups with the pteridosperms being in the latter category. The characters of the pteridosperm stem genera are given, and it is emphasized that they constitute a clearly defined group irrespective of the lack of knowledge as to whether they bore seeds or sporangia.

2. A new unique plant based on a stem with pteridosperm characters is described and discussed. Named *Microspermopteris aphyllum* because of its very small size and leafless condition it offers evidence for the origin of the seed-ferns from the Psilophytales, as well as for megaphyllous leaf development. It combines characters of both *Lyginopteris* and *Heterangium* and appears to have possibly been ancestral to both.

3. Three new species of *Medullosa* are described, and a new phylogenetic viewpoint presented. The evidence for a climbing or creeping habit for the group is given, new evidence being offered for a bilateral, dorsi-ventral habit.

4. Some excellent new material of *Medullosa Noei* is described with particular reference to new data on the conspicuous phloem rays, adventitious aerenchymatous roots, and periderm or "cambial" rings which appear similar to the star rings of the Permian species. "Star rings" are discussed in general, and it is shown that the fourth small stele of *Medullosa centrofilis* had nothing in common with the "star rings" of the Permian plants. "Aggregate leaf traces" in *Medullosa Thompsonii* are described and compared to Permian "star rings."

5. The microsporangiate fructifications of *Medullosa* are discussed and two new species of *Dolerotheca* are described. Evidence is offered that they constitute the most primitive of the known species and show additional proof of a radial rather than cyclic arrangement of the tubular sporangia. A very close association with possible attachment is illustrated for a *Dolerotheca* and *Myleoxylon*. It is also suggested that the plant remains from the Iowa coal balls may be of some aid in a more accurate determination of the horizon of the Des Moines Series.

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Explanation of Plate

PLATE 2

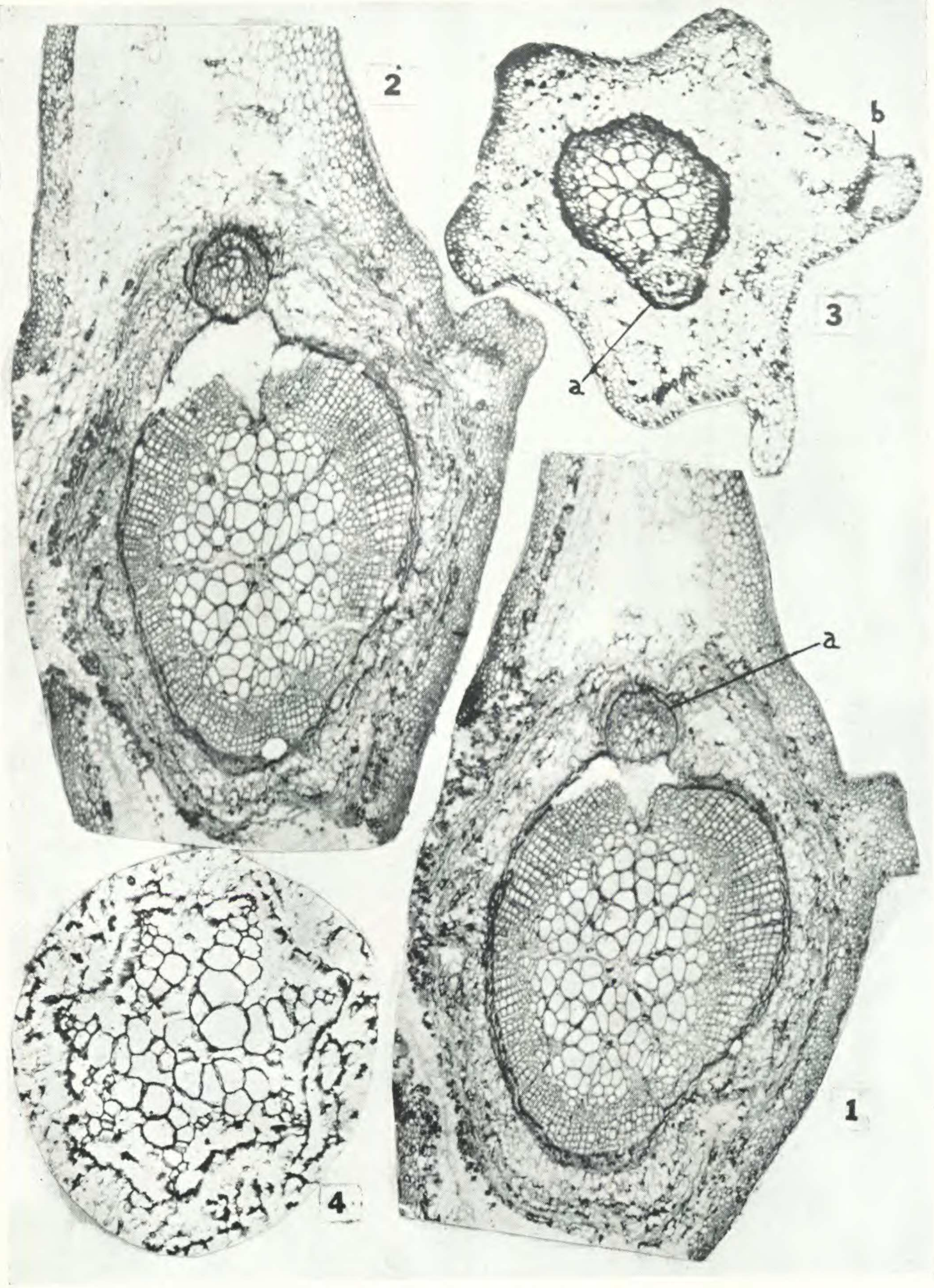
Microspermopteris aphyllum

Fig. 1. Cross-section of a mature stem showing departure of a collateral branch bundle. From slide 1602, × 20.

Fig. 2. Same specimen a few peels above the preceding figure. Branch bundle is becoming concentric. From slide 1603, × 20.

Fig. 3. Cross-section of a small stem (branch?): *a*, beginning of branch vascular bundle departure; *b*, sclerotic plate. (See fig. 55 which shows a later stage of branch bundle departure on same stem). From slide 1604, × 20.

Fig. 4. Enlargement of the stele of a heptarch adventitious root. (See fig. 56 for appearance of complete cross-section). From slide 1605, × 50.



BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

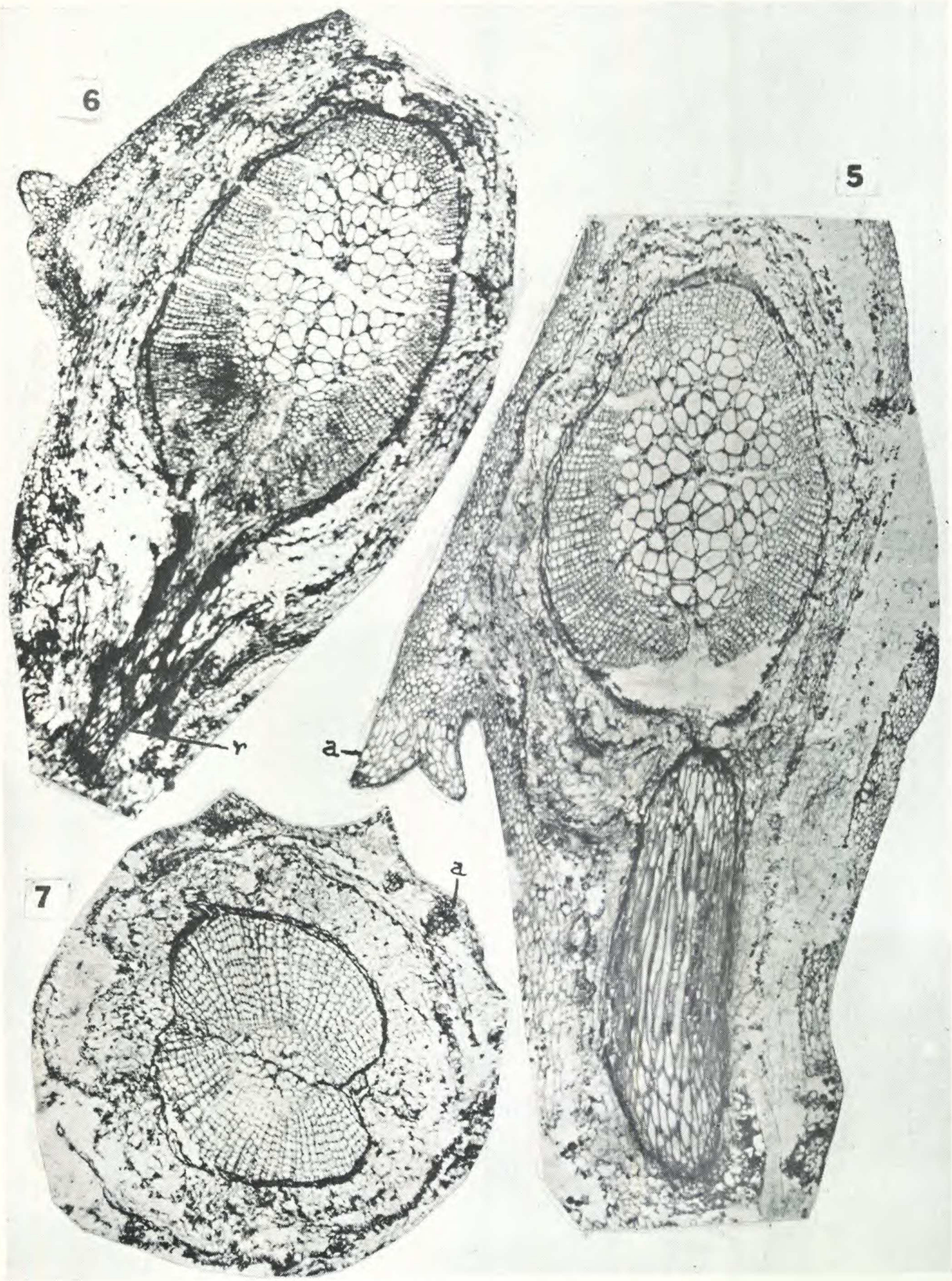
PLATE 3

Microspermopteris aphyllum

Fig. 5. Cross-section of same stem as in figs. 1 and 2, showing the horizontal passage of the branch vascular bundle; *a*, forked emergence. From slide 1606, × 18.

Fig. 6. Cross-section taken a few peels above the preceding figure showing departure of an adventitious root; root *(r)* has curved downwards and out of the cortex. From slide 1607, × 18.

Fig. 7. Cross-section of a more mature stem showing unequal xylem development; *a*, sclerotic plate just within the epidermis. From slide 1608, × 15.



BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 4

Microspermopteris aphyllum

Fig. 8. Radial section of stem: x^2, secondary xylem; *IC*, inner cortex; *OC*, outer cortex; *SP*, sclerotic plate; *em*, emergence. From slide 1609, × 50.

Fig. 9. Tangential view of secondary wood showing small uniseriate rays and pitting in tangential walls. From slide 1610, × 135.

Fig. 10. Radial section of stem showing sclerotic plates in outer cortex just within epidermis. From slide 1611, × 53.

Fig. 11. Tangential section through outer cortical zone showing anastamosing horizontal plates. From slide 1612, × 25.

Fig. 12. Reticulate bordered pitting in wall of a metaxylem tracheid. From slide 1613, × 450.

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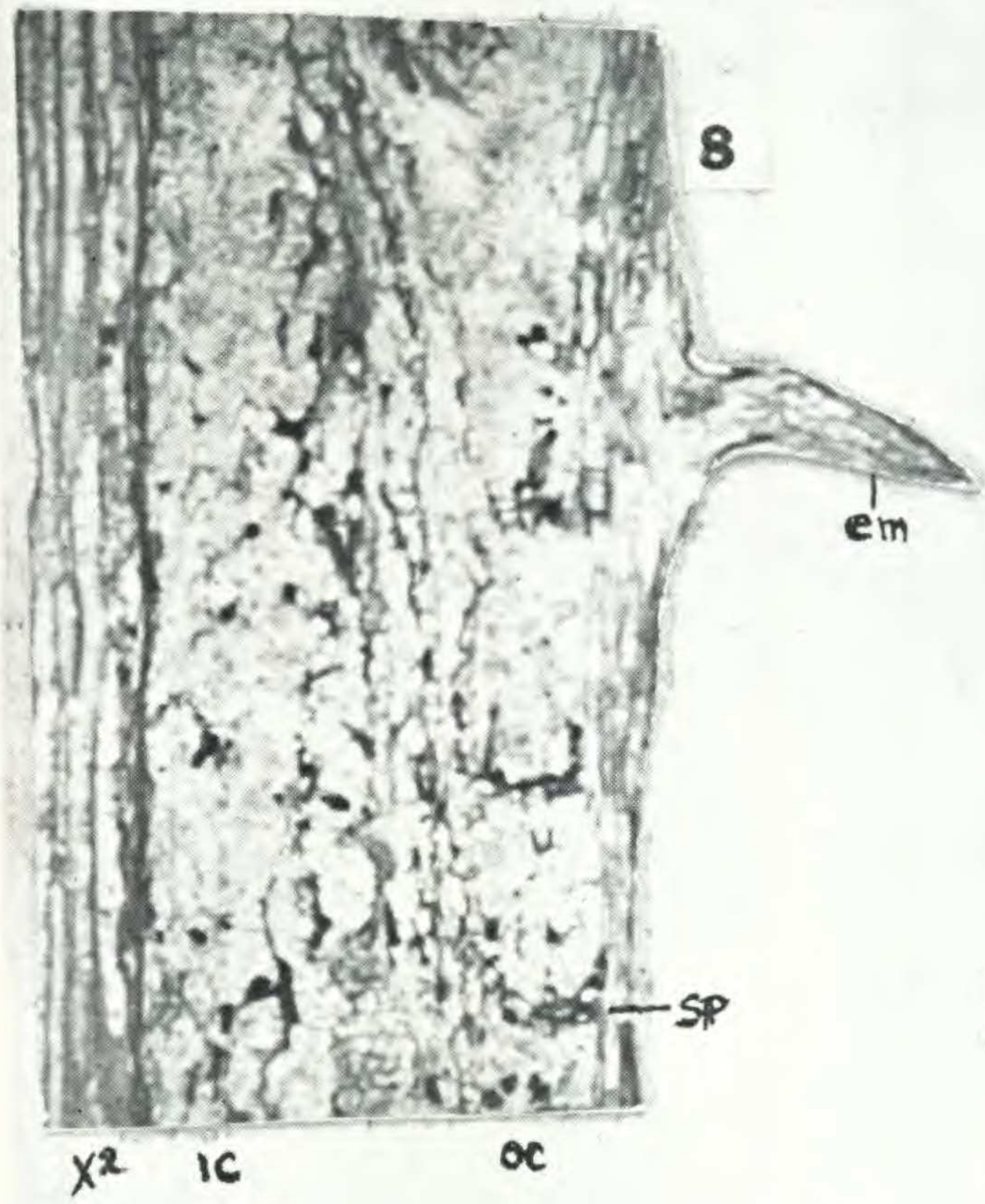

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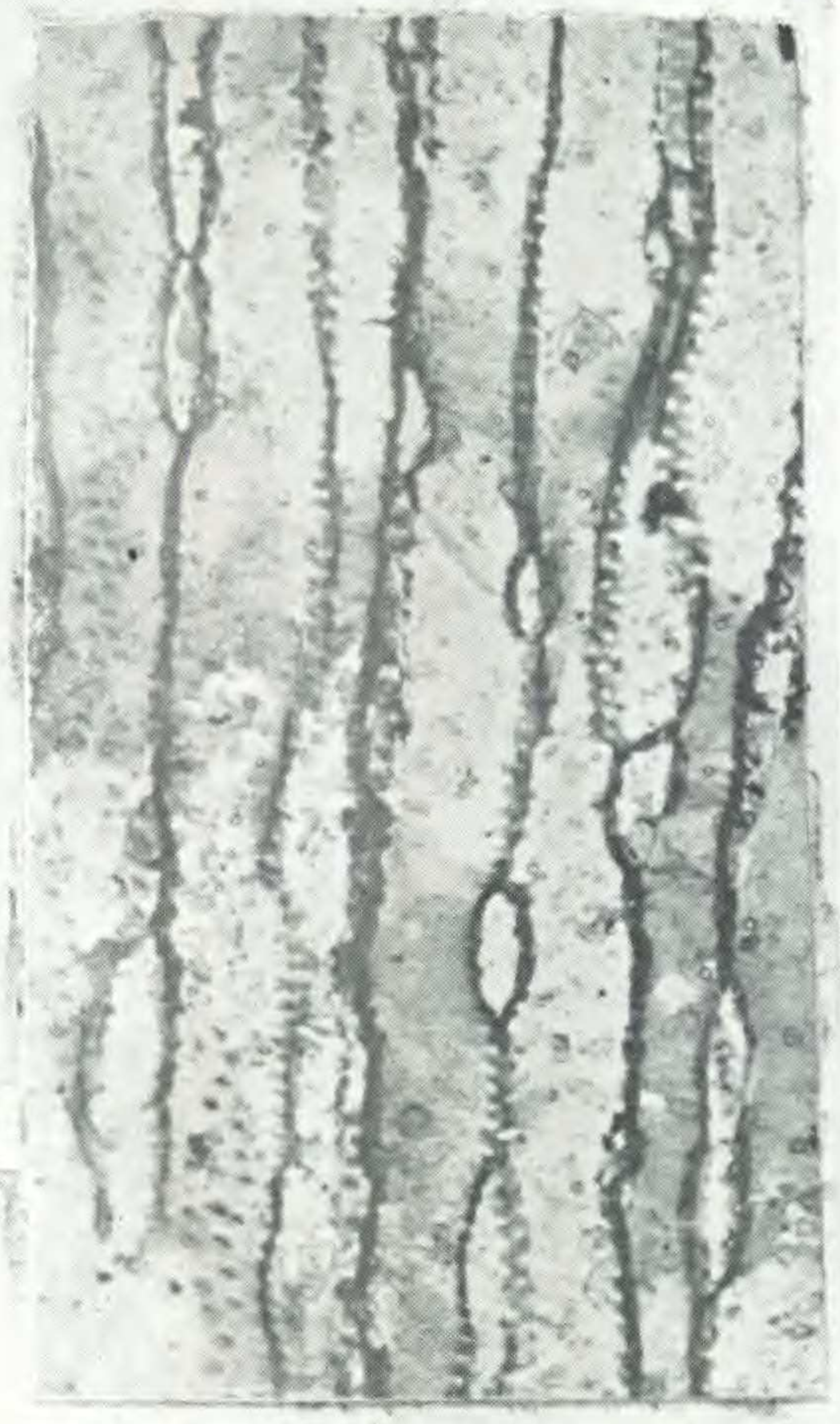

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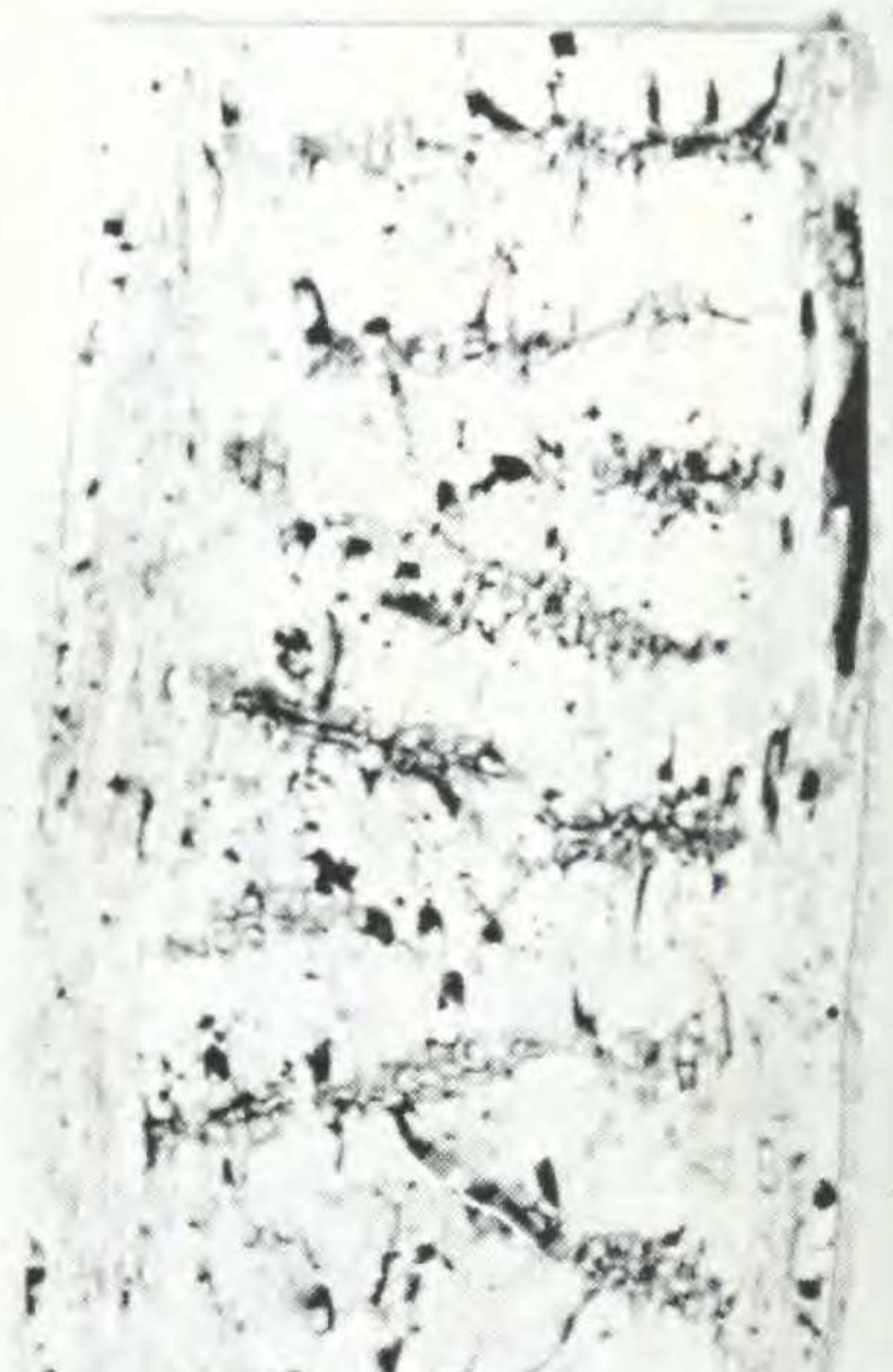

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BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 5

A partial reconstruction of *Microspermopteris aphyllum*, × 4. Explanation in text.

BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

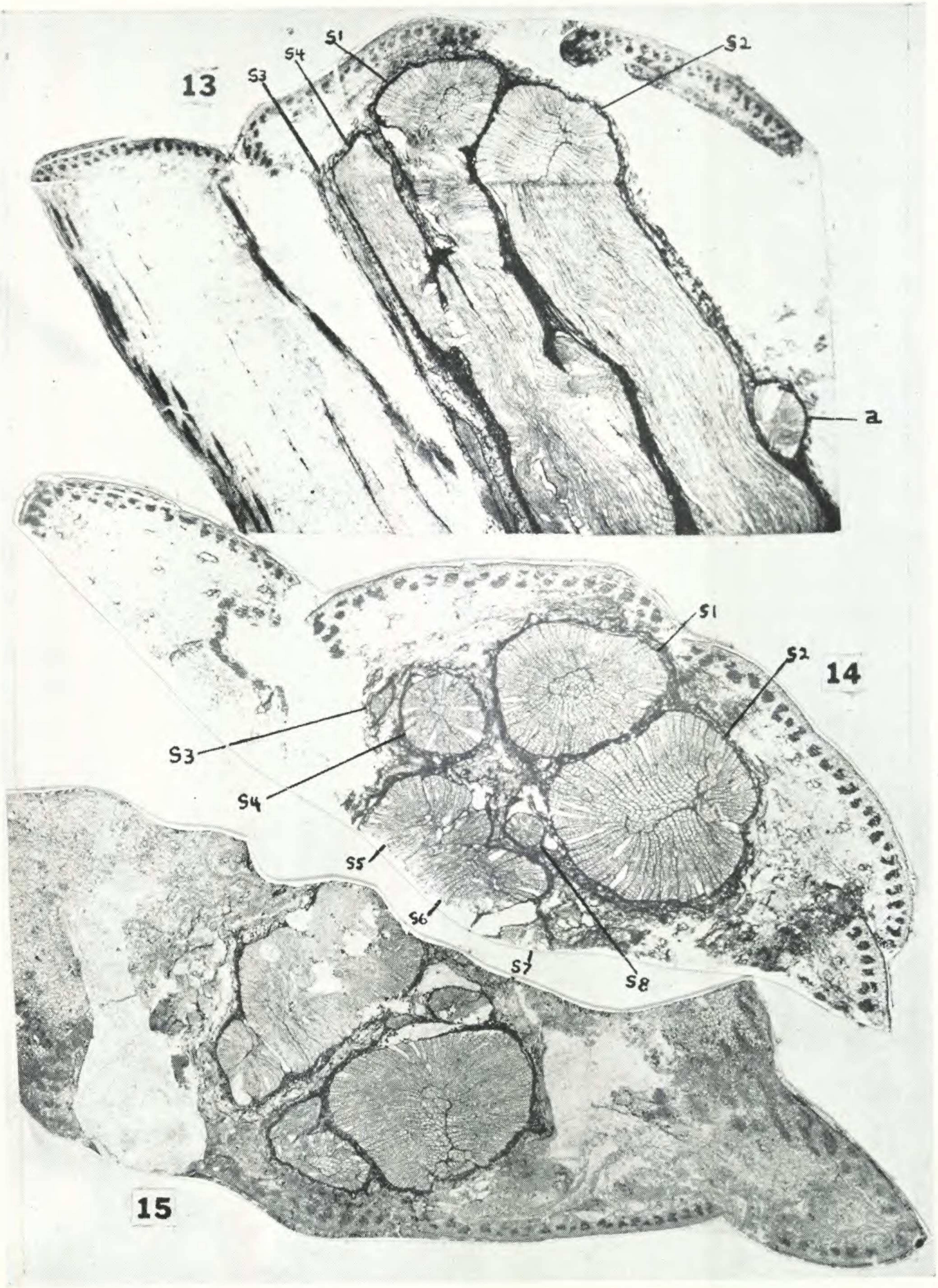
PLATE 6

Medullosa primaeva

Fig. 13. Transverse-longitudinal view of type specimen showing branching and fusing of the steles: *a*, small stele in a horizontal course through the stem; *S1*, *S2*, *S3*, and *S4* show portions of steles indicated in next figure. From slide 1614, × 4.5.

Fig. 14. Transverse section of top surface of type specimen: *S1*, *S2*, *S3*, *S4*, *S5*, *S6*, *S7*, and *S8* indicate the eight steles. From slide 1615, × 6.2.

Fig. 15. Transverse section of bottom surface of type specimen. Steles have partially fused. From slide 1616, × 6.2.



BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 7

Medullosa elongata

Fig. 16. Transverse view of complete type specimen: *a* and *b*, lateral leaf bases; *c*, dorsal leaf base. From slide 1617, × 2.5.

Fig. 17. Enlargement of central portion of stem shown in fig. 16 to show the details of the three steles. Note narrow line of primary wood in lower left-hand stele. From slide 1617, × 6.5.

Fig. 18. Compound resin canals which run horizontally through the stem. From slide 1618, × 6.5.

Medullosa primaeva

Fig. 19. Enlargement of steles *S1* and *S2* from fig. 14. Note almost solid protosteles. From slide 1615, × 16.

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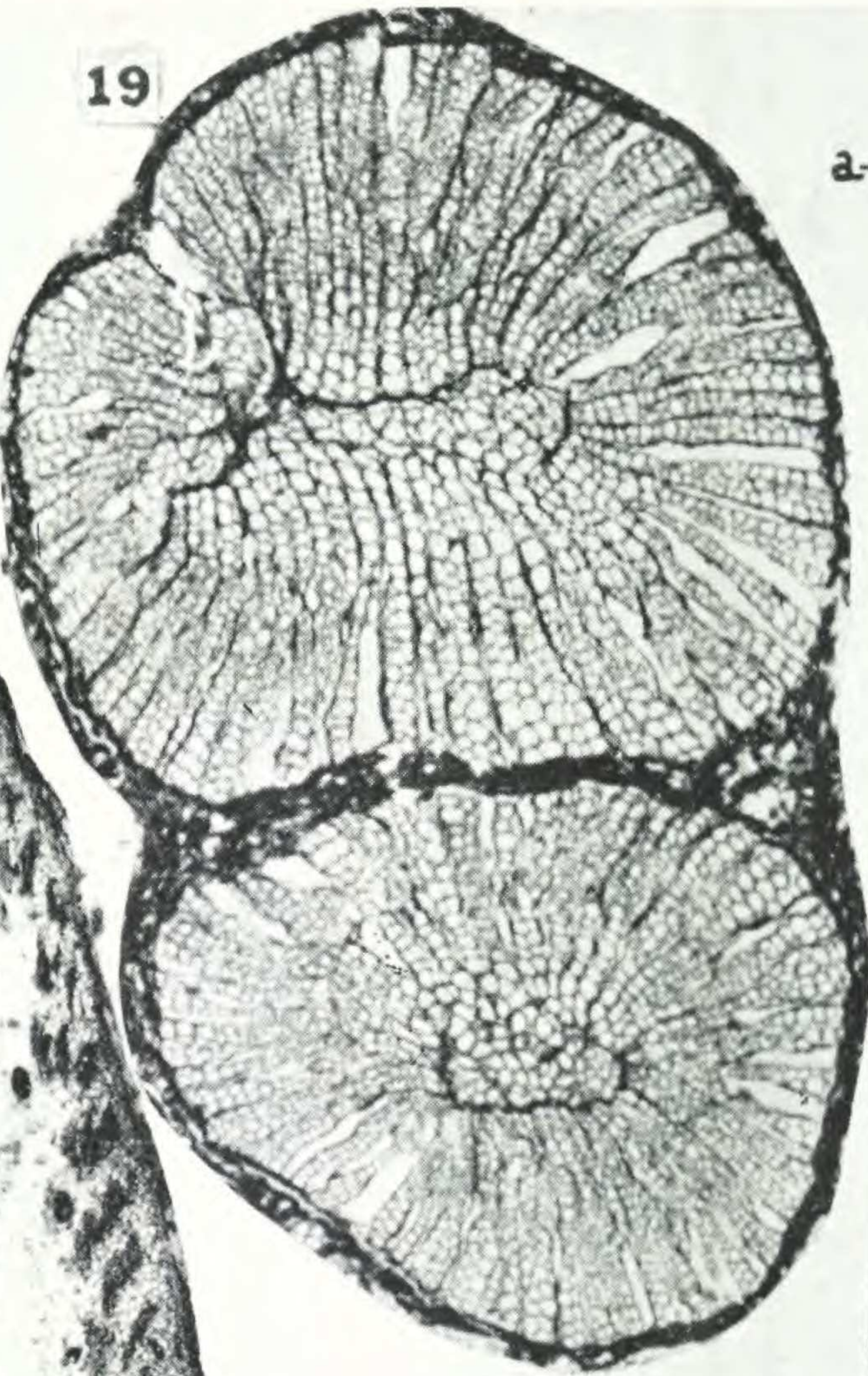

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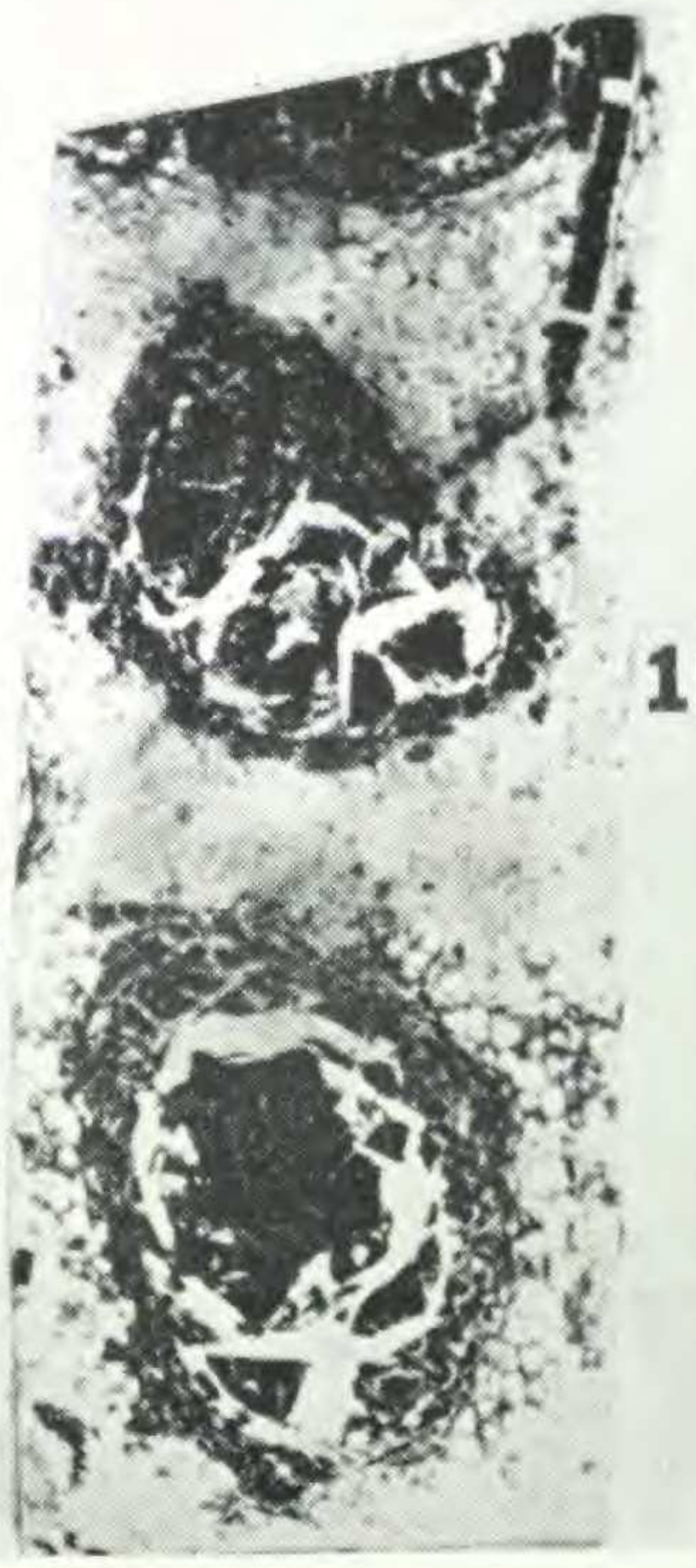

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Explanation of Plate

PLATE 8

Medullosa endocentrica

Fig. 20. Transverse section of stelar assembly of type specimen with enclosing "periderm": *a*, third small stele; *b*, phloem zone; *X1*, primary xylem. From slide 1619, × 10.

Fig. 21. Transverse-tangential section showing very broad rays in "phloem" area. Above point indicated by *(a)* is transverse, below tangential. From slide 1620, × 40.

Fig. 22. Tangential-transverse section through secondary xylem showing narrow (1–2 cells wide) rays; *a* indicates line between transverse and tangential views. From slide 1621, × 40.

Fig. 23. Portion of a transverse "sieve plate" from one of the large "sieve tubes" of the phloem zone. From slide 1620, × 650.

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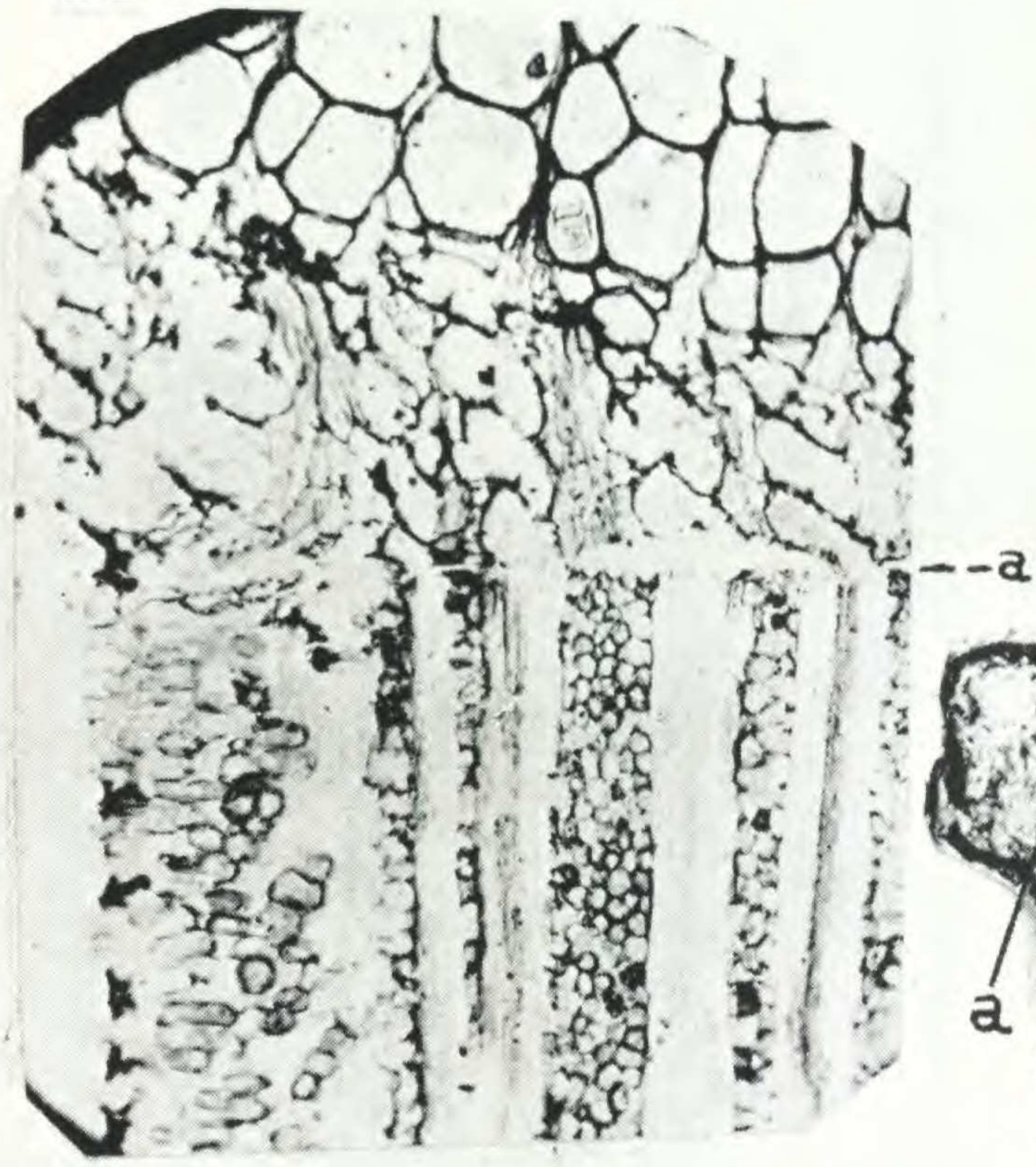

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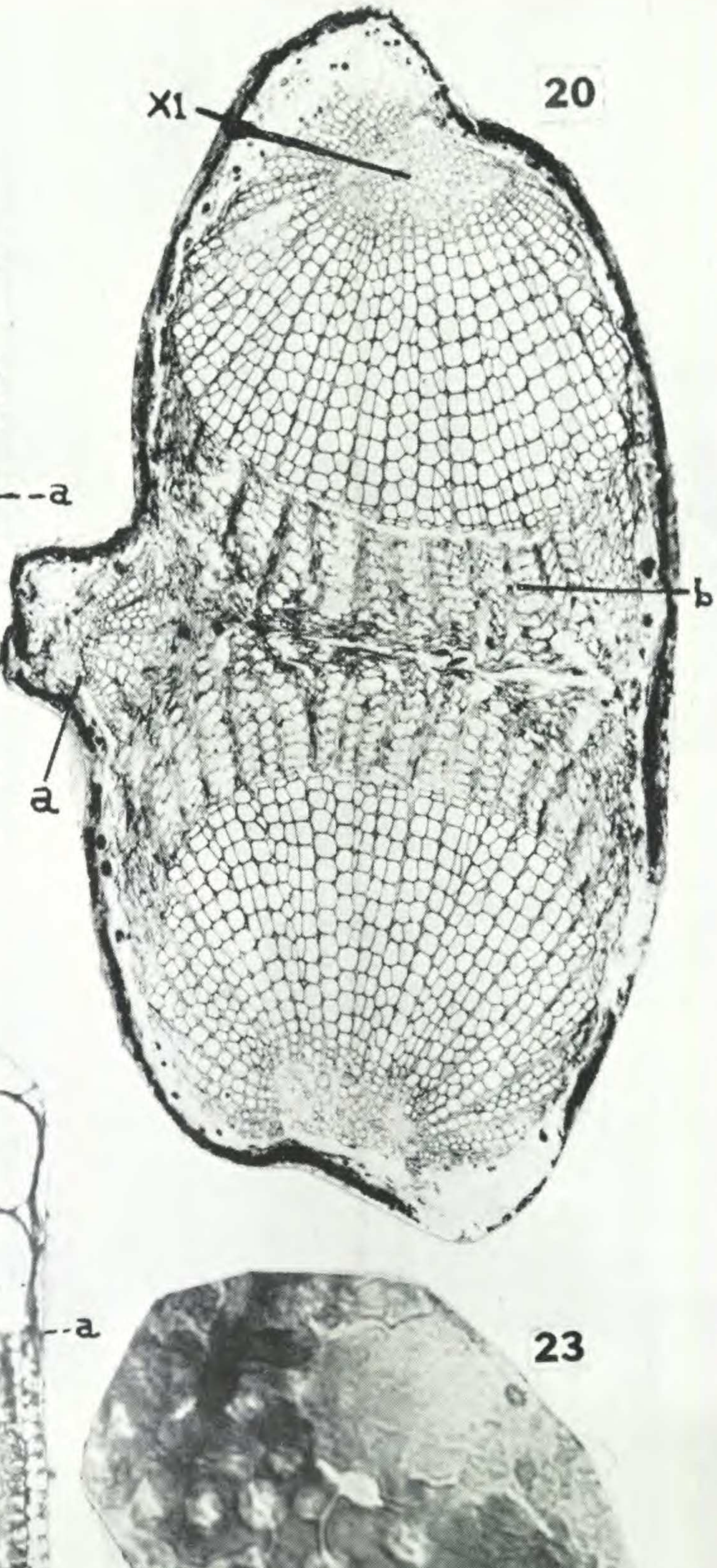

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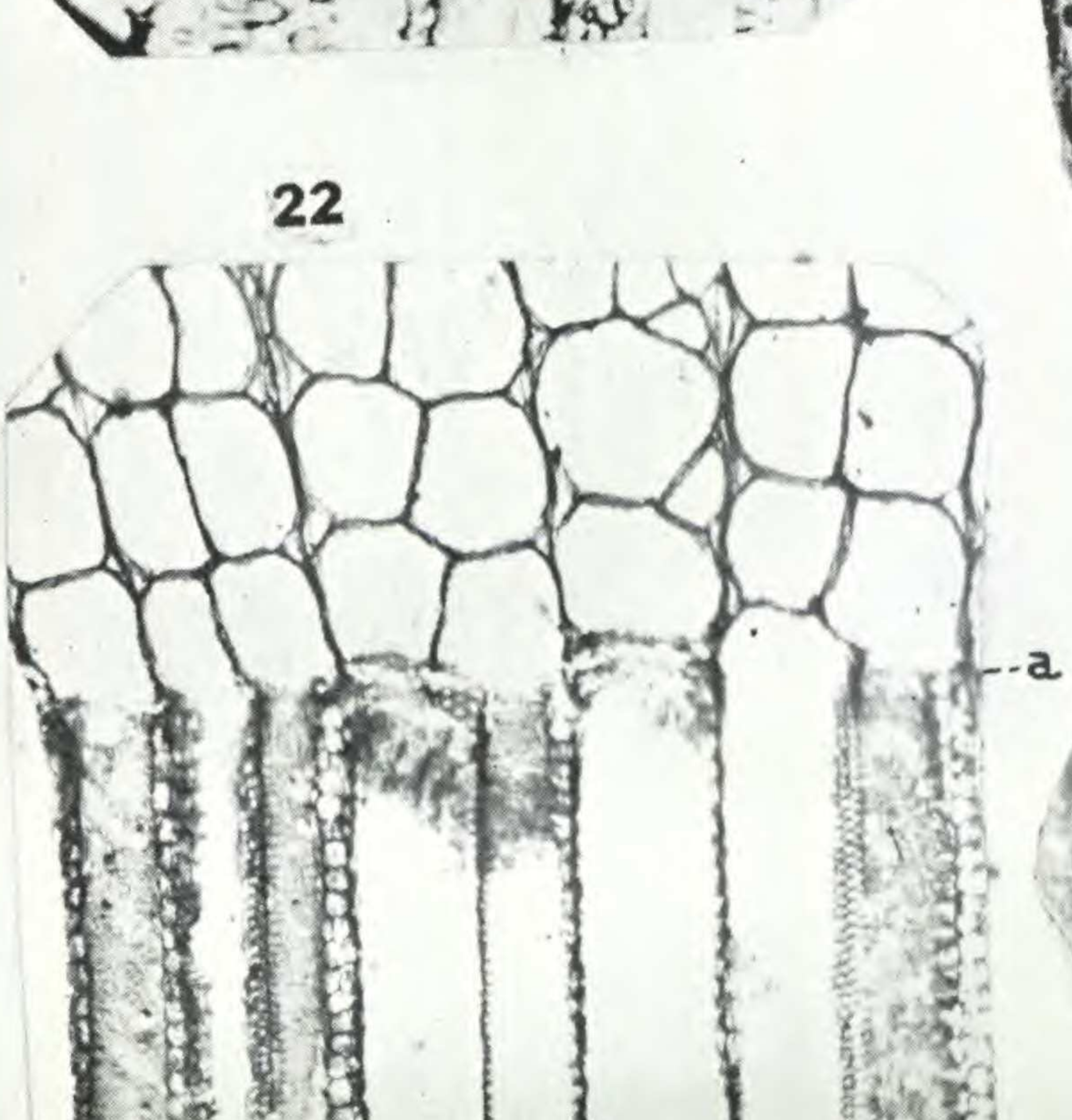

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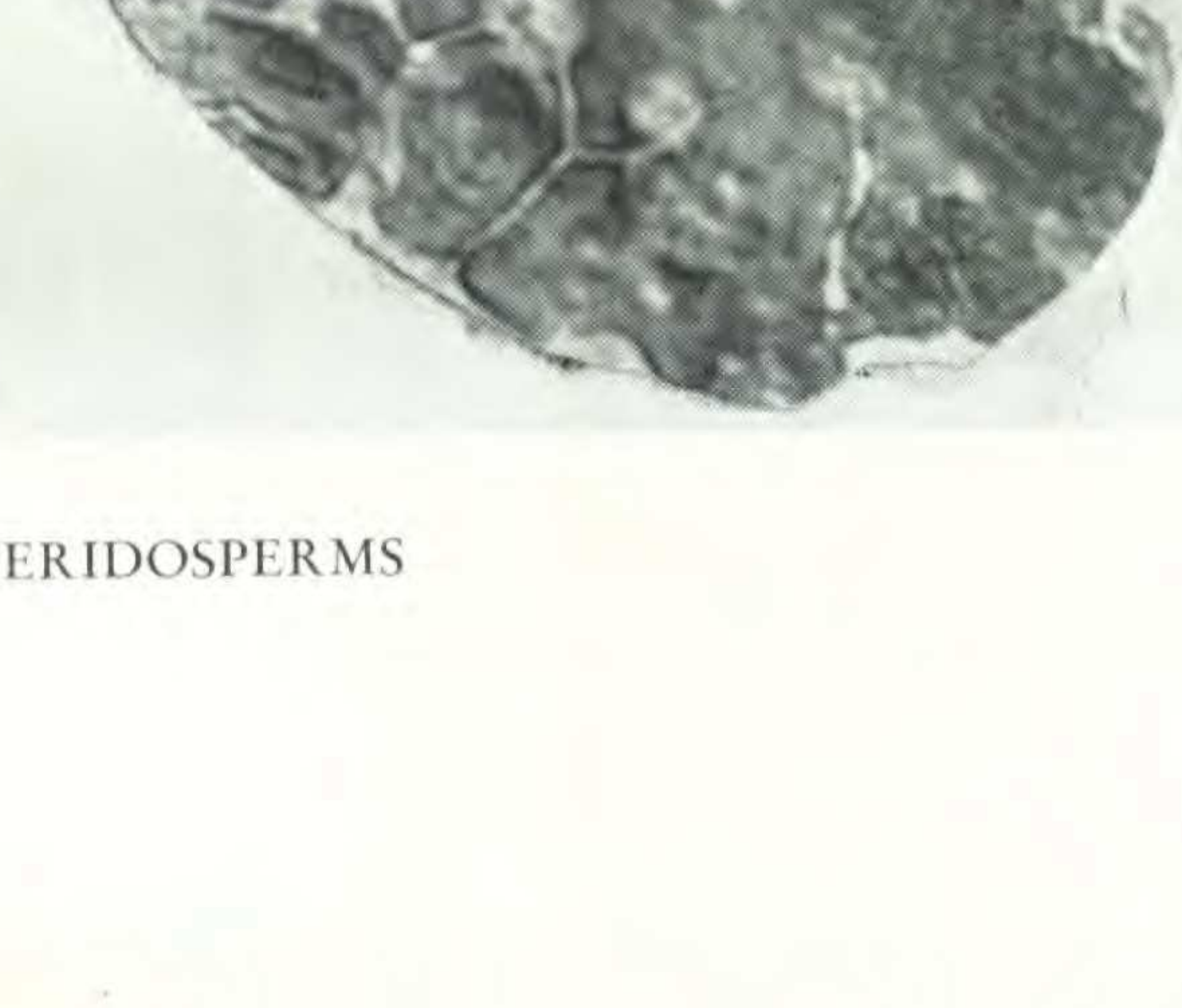


BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 9

Medullosa Noei

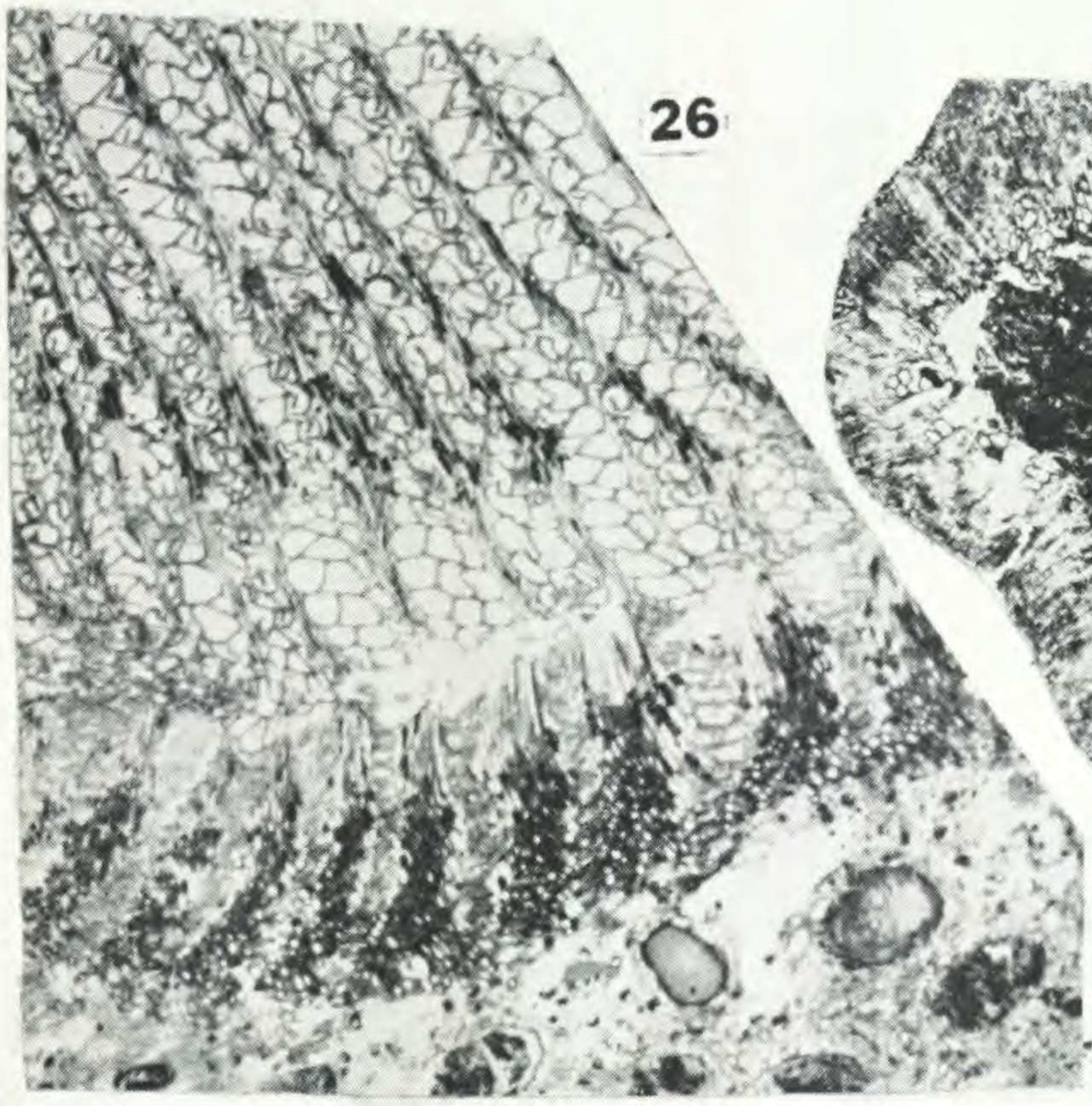
Fig. 24. A single "cambial ring" showing development of secondary wood. Dark central area is composed of primary tracheids and parenchyma. From slide 1622, × 9.

Fig. 25. A single well-preserved cortical, pentarch root. Note enclosing periderm and aerenchymatous cortex. From slide 1623, × 14.

Fig. 26. Marginal portion of a stele showing fringe of expanded phloem rays. From slide 1624, × 12.

Medullosa primaeva

Fig. 27. Longitudinal section through cortex showing spiral thickening in a leaf trace. From slide 1625, × 95.



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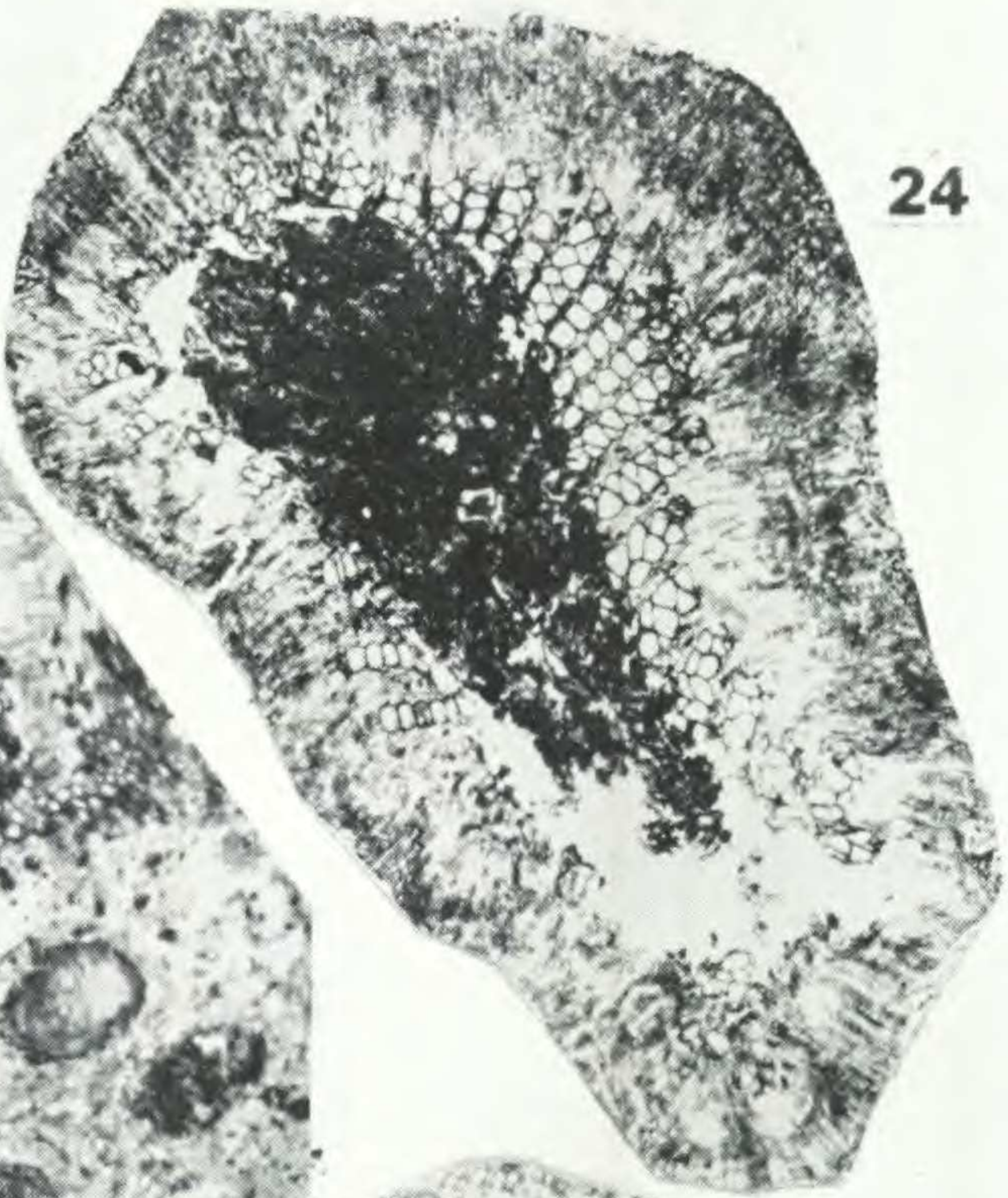

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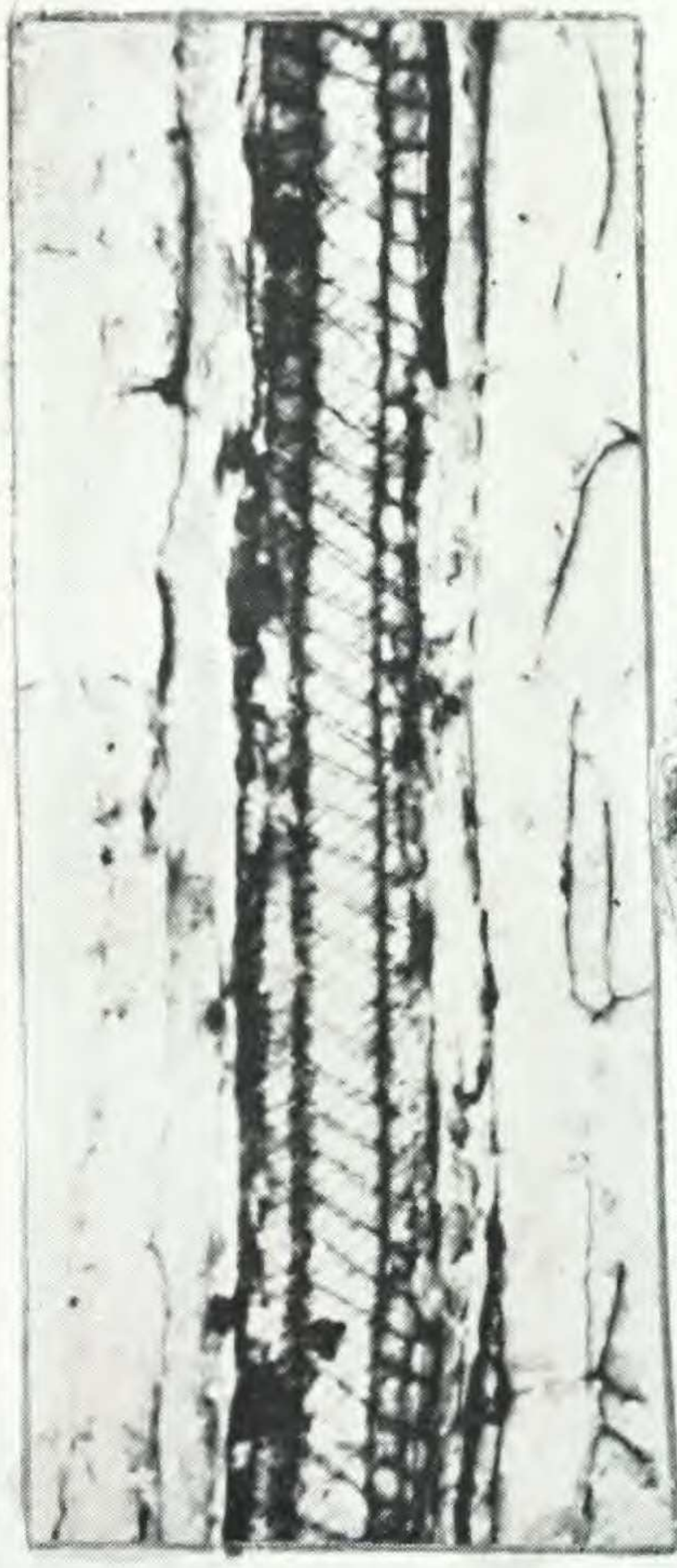

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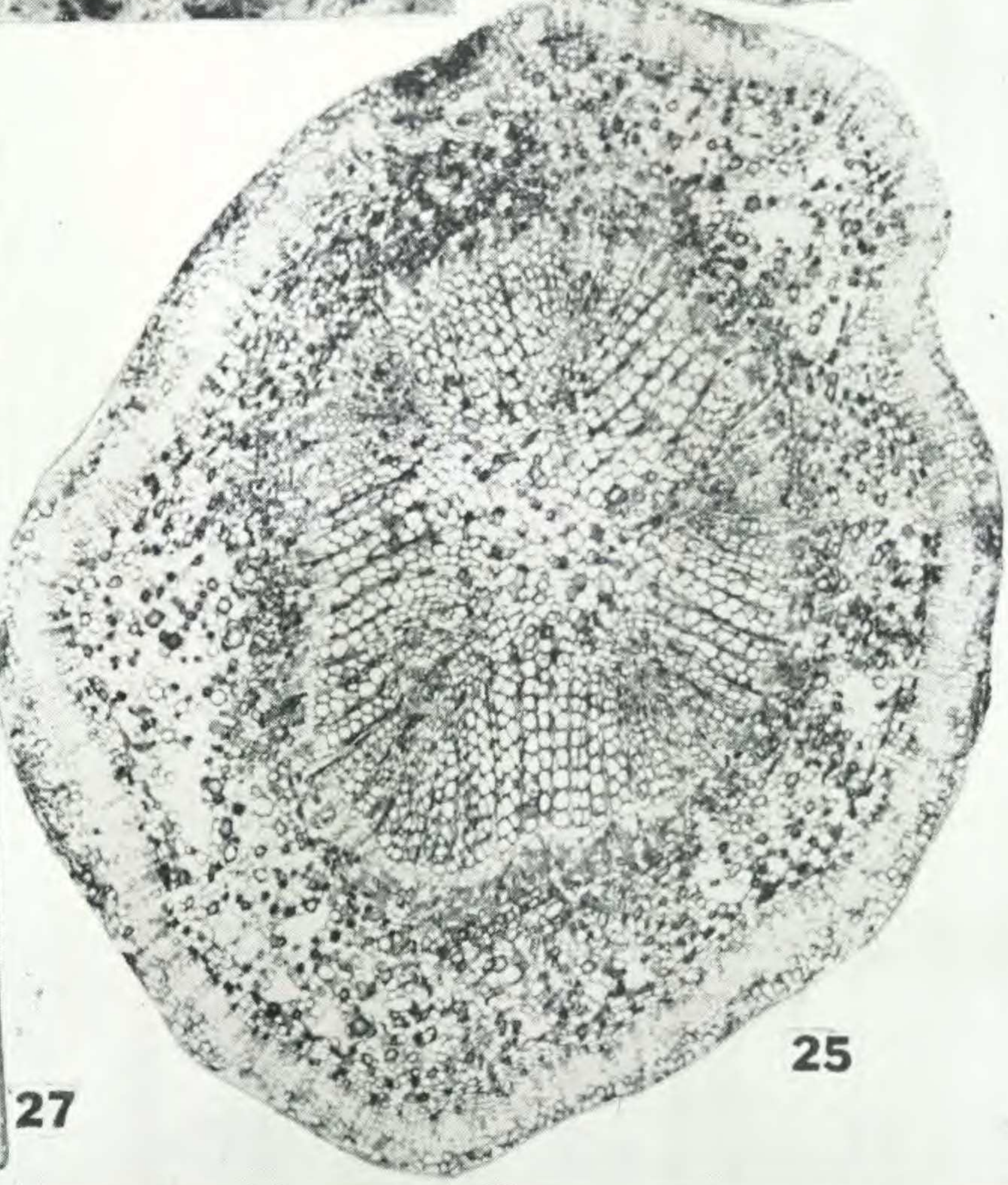

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Explanation of Plate

PLATE 10

"Star Rings"

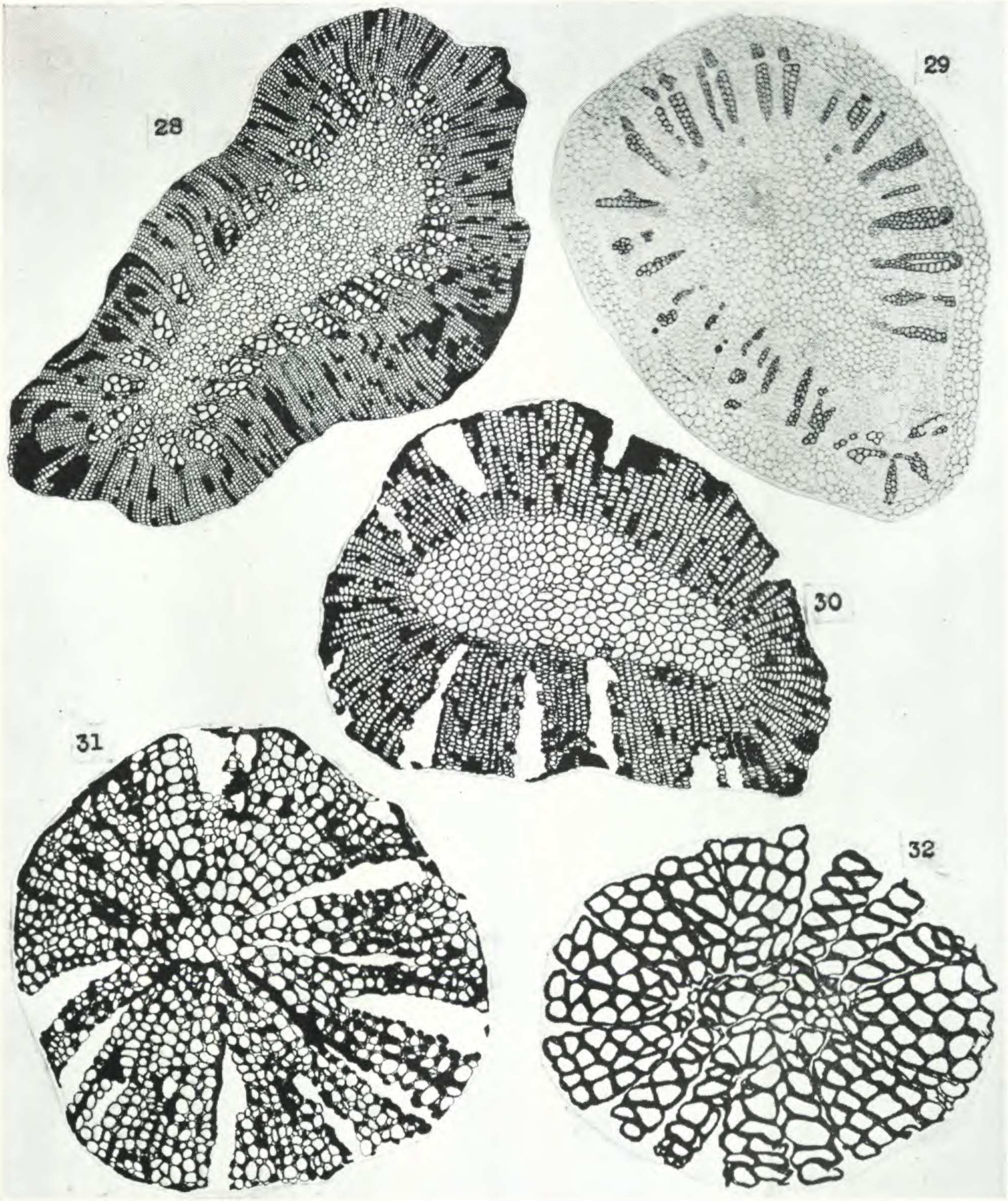
Fig. 28. A "cambial" or "periderm" ring from M. *Noei* in which radial rows of secondary xylem have formed. From slide 1622, × 5.5.

Fig. 29. A "star ring" from M. *stellata* v. Cotta a. *typica*, at the same magnification as the above (after Weber and Sterzel), × 5.5.

Fig. 30. An "aggregate leaf trace" from M. *Thompsonii* (see fig. 59b). From slide 1626, × 13.7.

Fig. 31. A single small stele of M. *primaeva*. From slide 1615, × 20.7.

Fig. 32. "Star Ring" of M. *centrofilis* (after De Fraine), × 20.7.



BAXTER—FOSSIL PTERIDOSPERMS

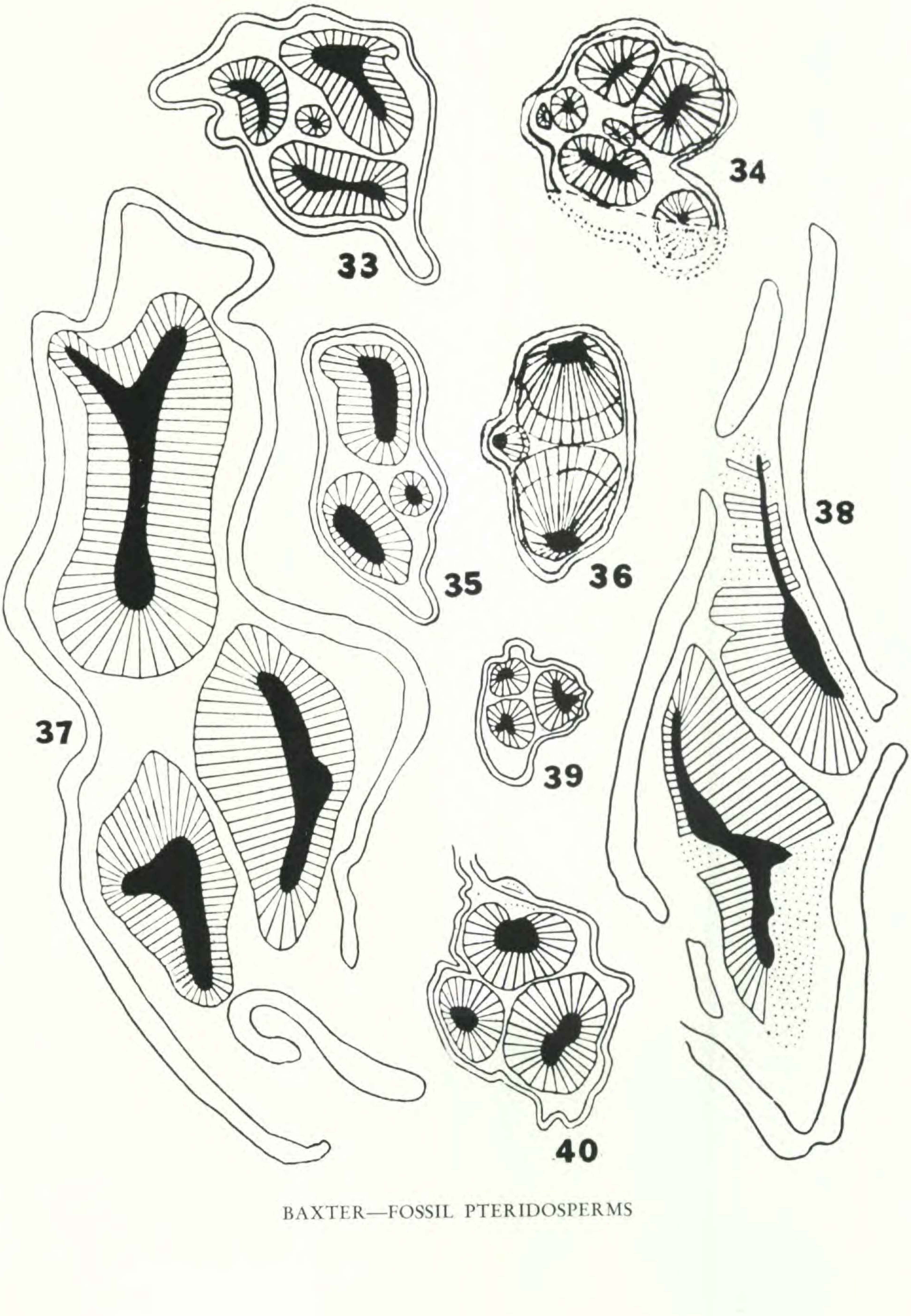
Explanation of Plate

PLATE 11

Diagrams of the stelar assemblies with enclosing periderm (where present) of all of the Carboniferous species of *Medullosa* with the exception of *M. Leuckarti.* The magnification is 2.8, and all of the diagrams other than figs. 34, 36, 42, and 43 are taken from Andrews (1945, 1946). The primary area of the stele is shown as solid black, the secondary wood as radiating lines, and the periderm as enclosing double or dotted lines depending on whether it was actually observed or was partially assumed.

Fig. 33. *M. centrofilis* De Fraine; Fig. 34. *M. primaeva* Baxter; Fig. 35. *M. Thompsonii* Andrews; Fig. 36. *M. endocentrica* Baxter; Fig. 37. *M. anglica* Scott; Fig. 38. *M. distelica* Schopf; Fig. 39. *M. pusilla* Scott; Fig. 40. *M. anglica* var. *Thiesseni* Schopf.

(Continued on pl. 12)

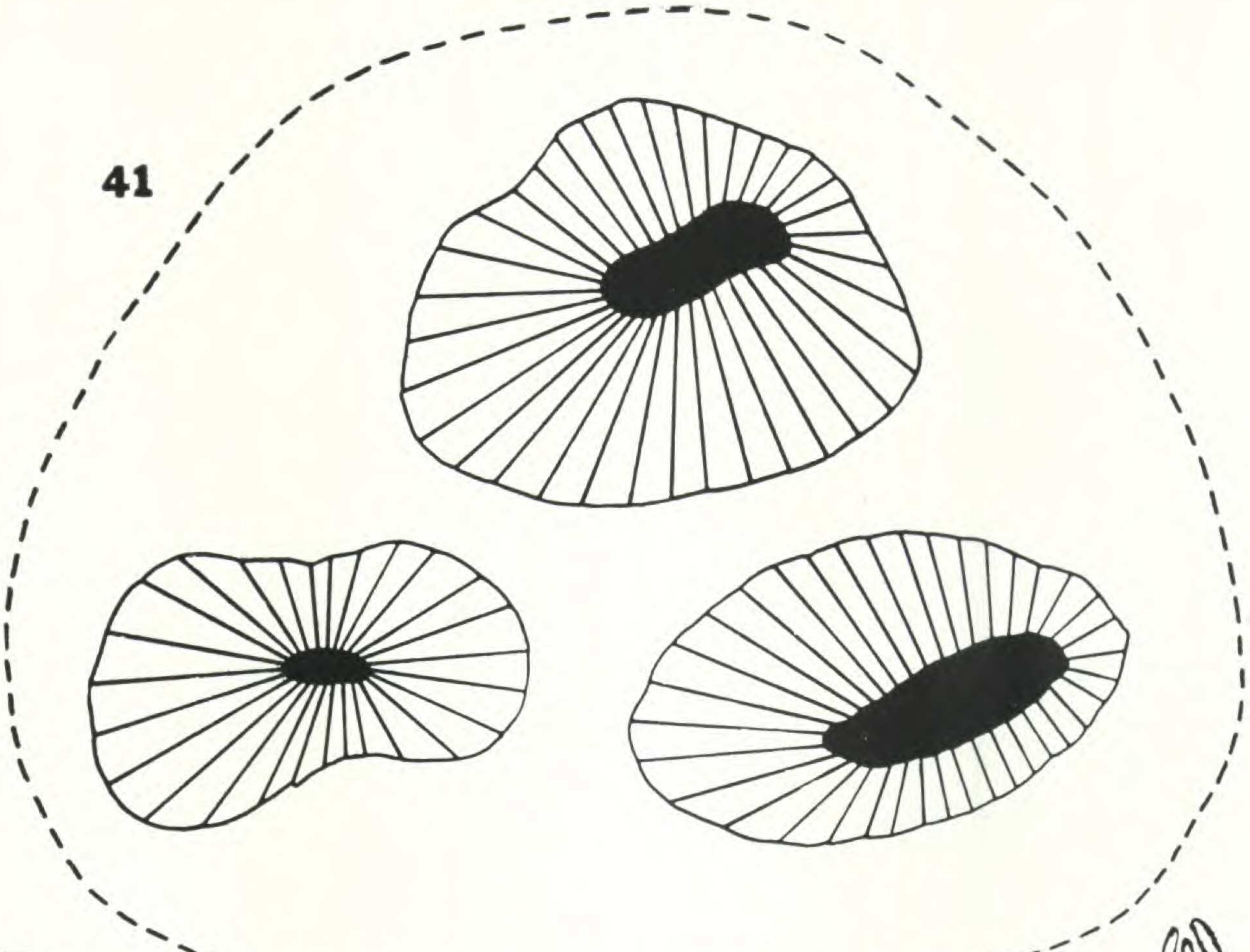


BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 12

Fig. 41. *M. anglica* var. *ioensis* Andrews; Fig. 42. *M. elongata* Baxter; Fig. 43. *M. Noei* Steidtmann, showing only about half of two of the stem's three steles. (*M. Noei* is so much larger than any of the other species represented here that one complete stele at × 2.8 magnification would more than fill an entire plate.) The white ring within the black primary area (in the upper of the two stele halves) represents a "cambial ring" as shown in figs. 24 and 28.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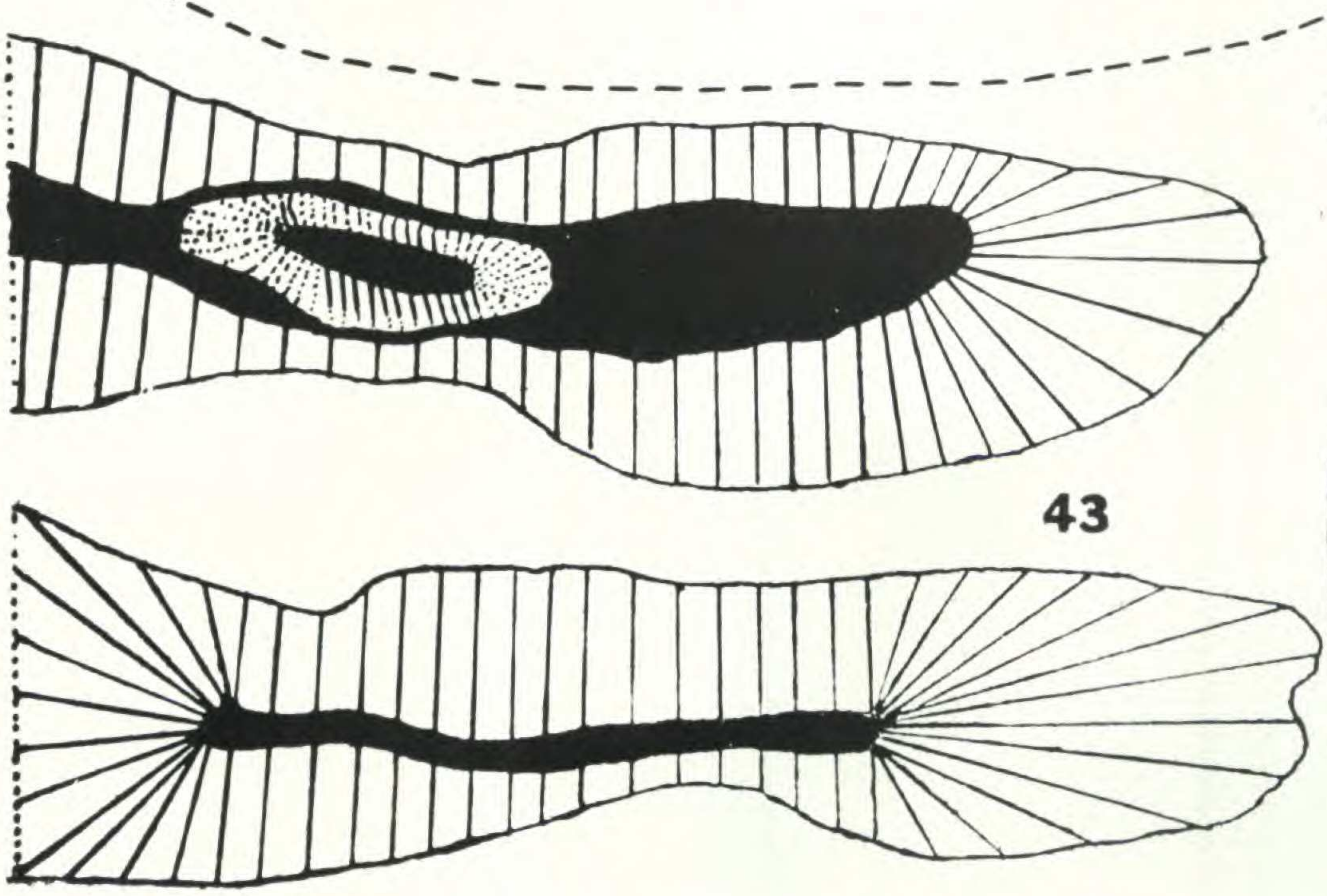
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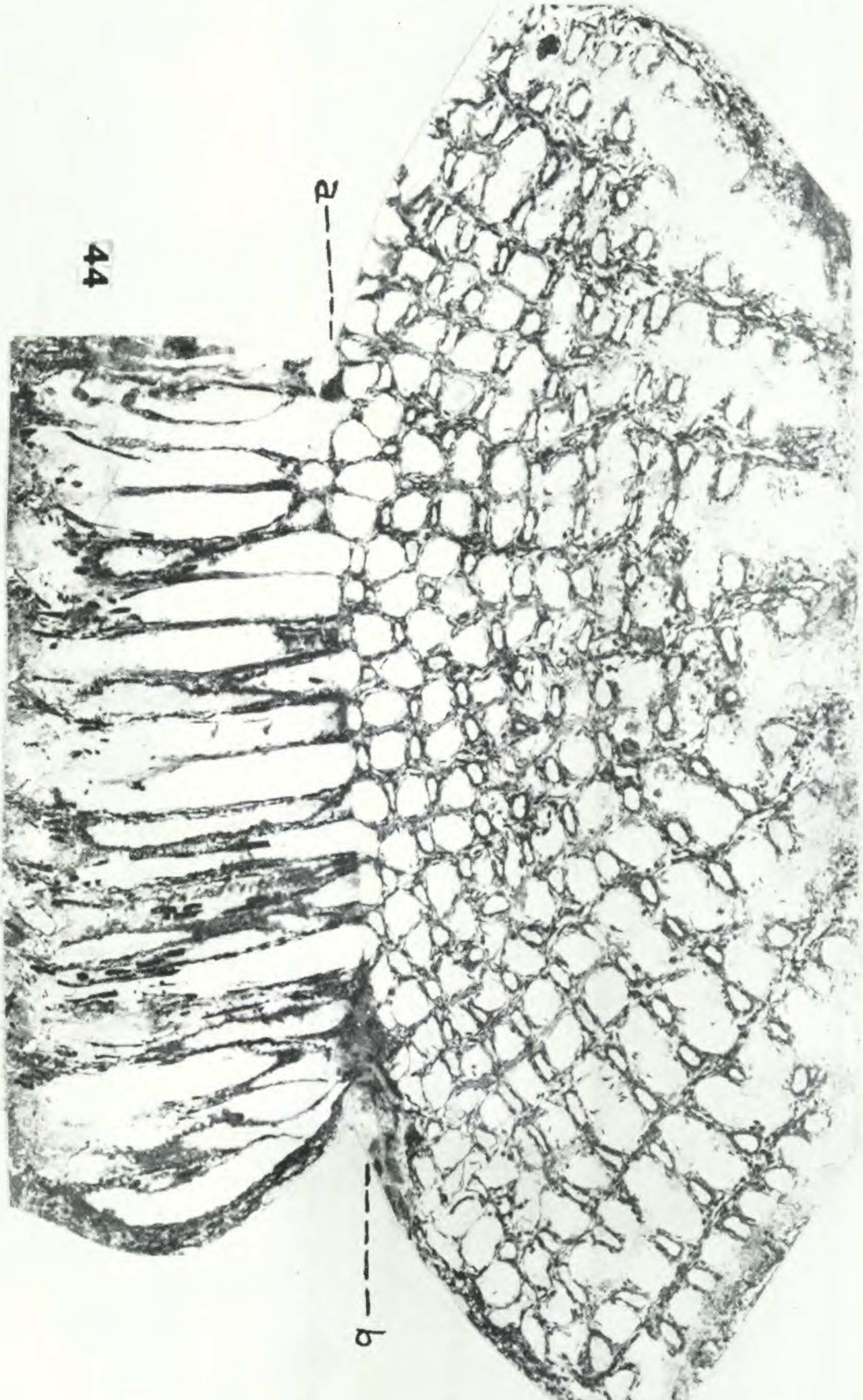
Explanation of Plate

PLATE 13

Dolerotheca formosa

Fig. 44. Transverse-longitudinal view of a portion of a complete campanulum. Below the line *a-b* is the longitudinal cut; above, the transverse. In comparison with the following figure note the large lysigenous tubes and absence of a strong sclerotic framework. From slide 1627, × 9.



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Explanation of Plate

PLATE 14

Dolerotheca sclerotica

Fig. 45. Transverse-longitudinal view of entire fructification. Below the line *a-b* is the longitudinal cut showing the curving of the marginal sporangia; above is the transverse cut showing the bifurcation of the thick sclerotic bands, between which can be seen the parenchymatous-secretory tissue forming the sporangial walls. The upper right-hand margin shows the sclerotic hypodermal zone. For more detailed view see figs. 48 and 49 from slide 1628, × 9.

BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

PLATE 15

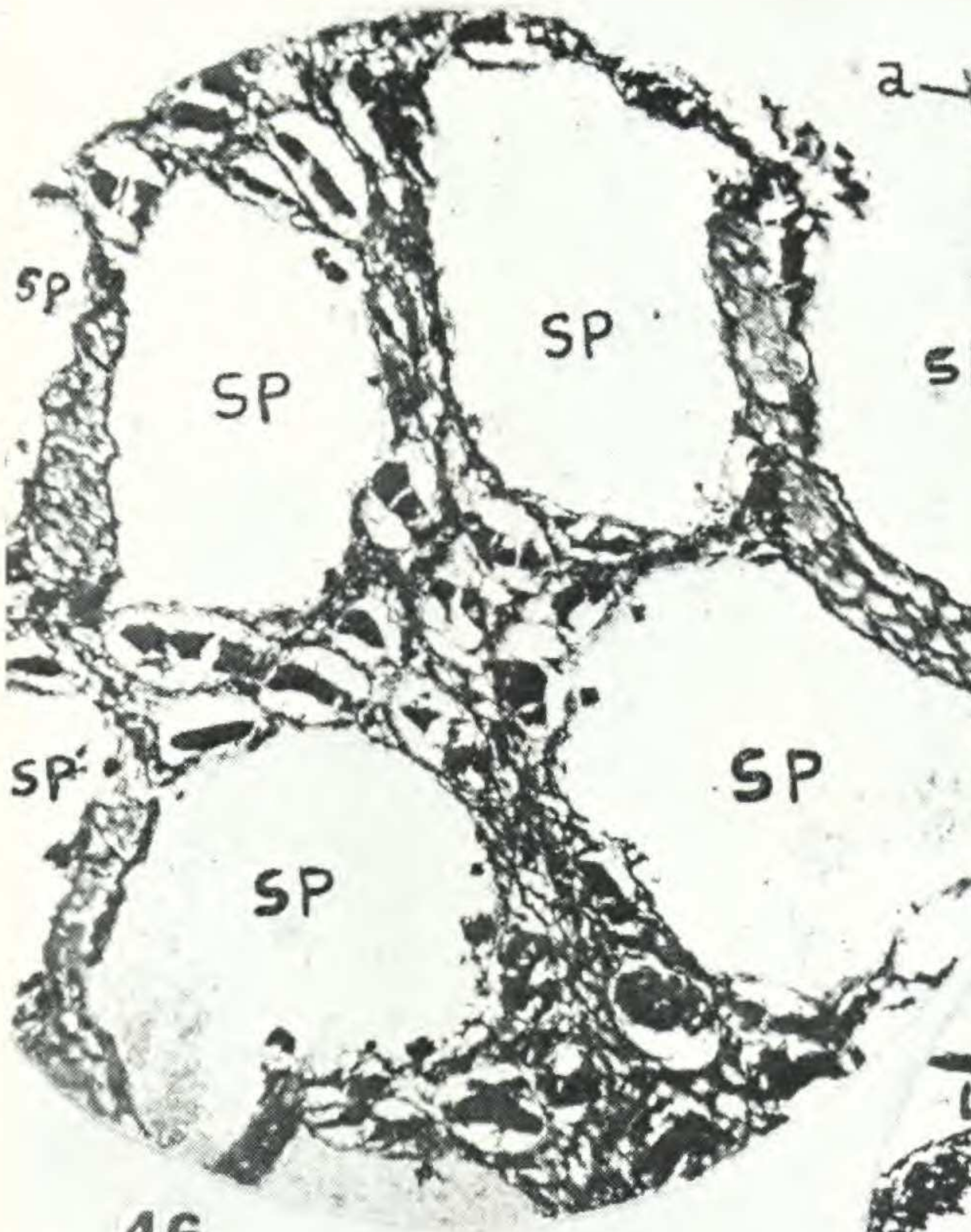
Fig. 46. *Dolerotheca Schopfii.* Transverse view of a double row of tubular sporangia showing four empty sporangia separated by the slime canal and sclerotic ground tissue and enclosed on the left and right by the thick sclerotic bands. Note absence of lysigenous tube between sporangia; *sp*, sporangium. From slide 1629, × 22.

Fig. 47. *Dolerotheca Schopfii.* Transverse view of campanulum wall showing pubescent epidermis and secretory-sclerotic hypodermal zone; *a*, glandular hairs. See fig. 57 for detail of hairs. From slide 1629, × 40.

Fig. 48. *Dolerotheca sclerotica.* Transverse view of a double row of sporangia separated from portions of two other rows by the thick sclerotic bands. Note thin-walled lysigenous tubes alternating radially with the sporangia and bifurcation of the sclerotic bands; *sp*, sporangia; *l*, lysigenous tubes. From slide 1628, × 32.

Fig. 49. *Dolerotheca sclerotica.* Transverse view of campanulum wall showing epidermis and sclerotic hypodermal zone; *sp*, sporangia. From slide 1628, × 40.

Fig. 50. *Dolerotheca formosa* Schopf. Transverse view of a double row of sporangia with the alternating smaller lysigenous tubes. *a* and *b* indicate the much less conspicuous sclerotic bands than in figs. 46 and 48; *sp*, sporangia; *l*, lysigenous tubes. From slide 1627, × 32.



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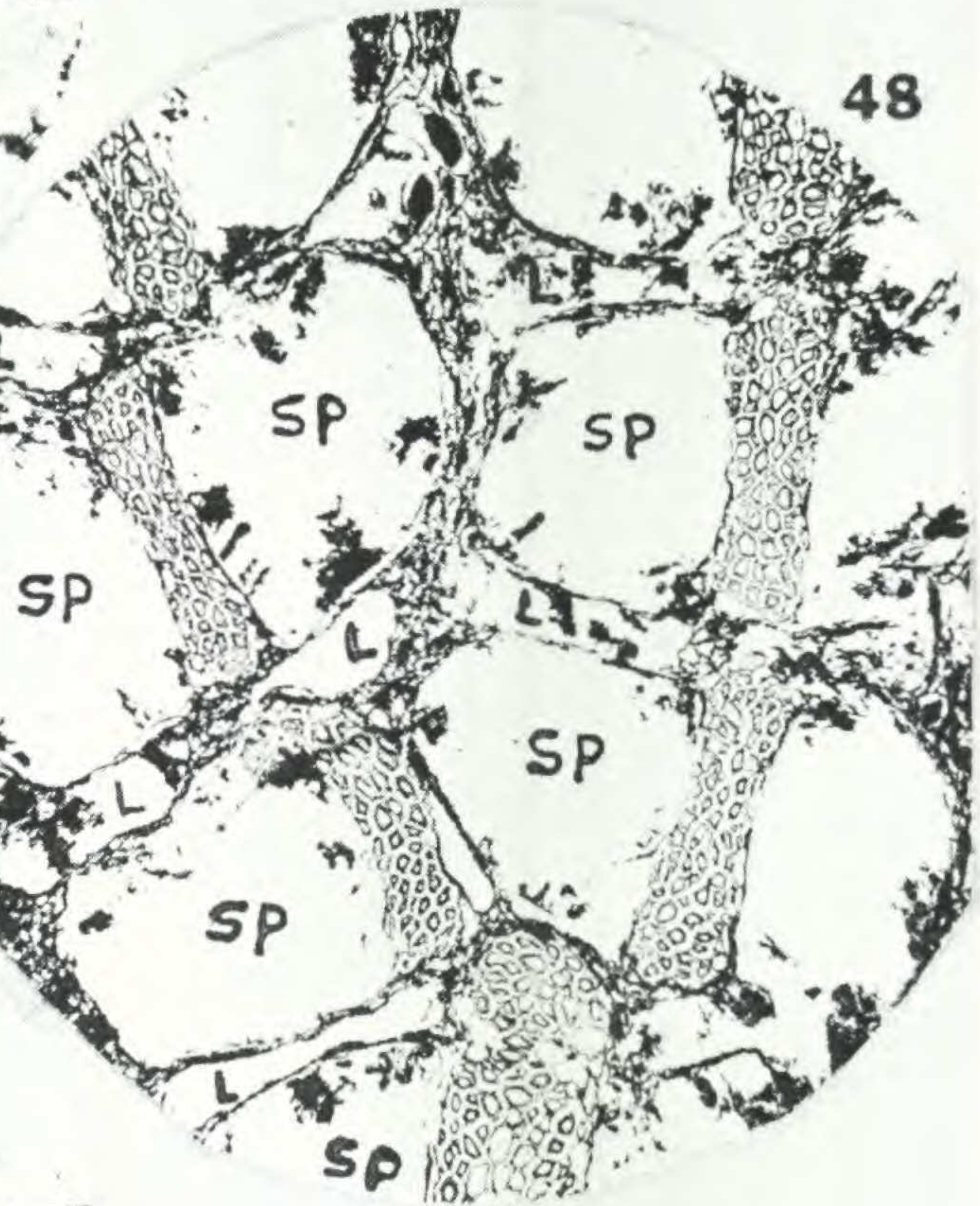

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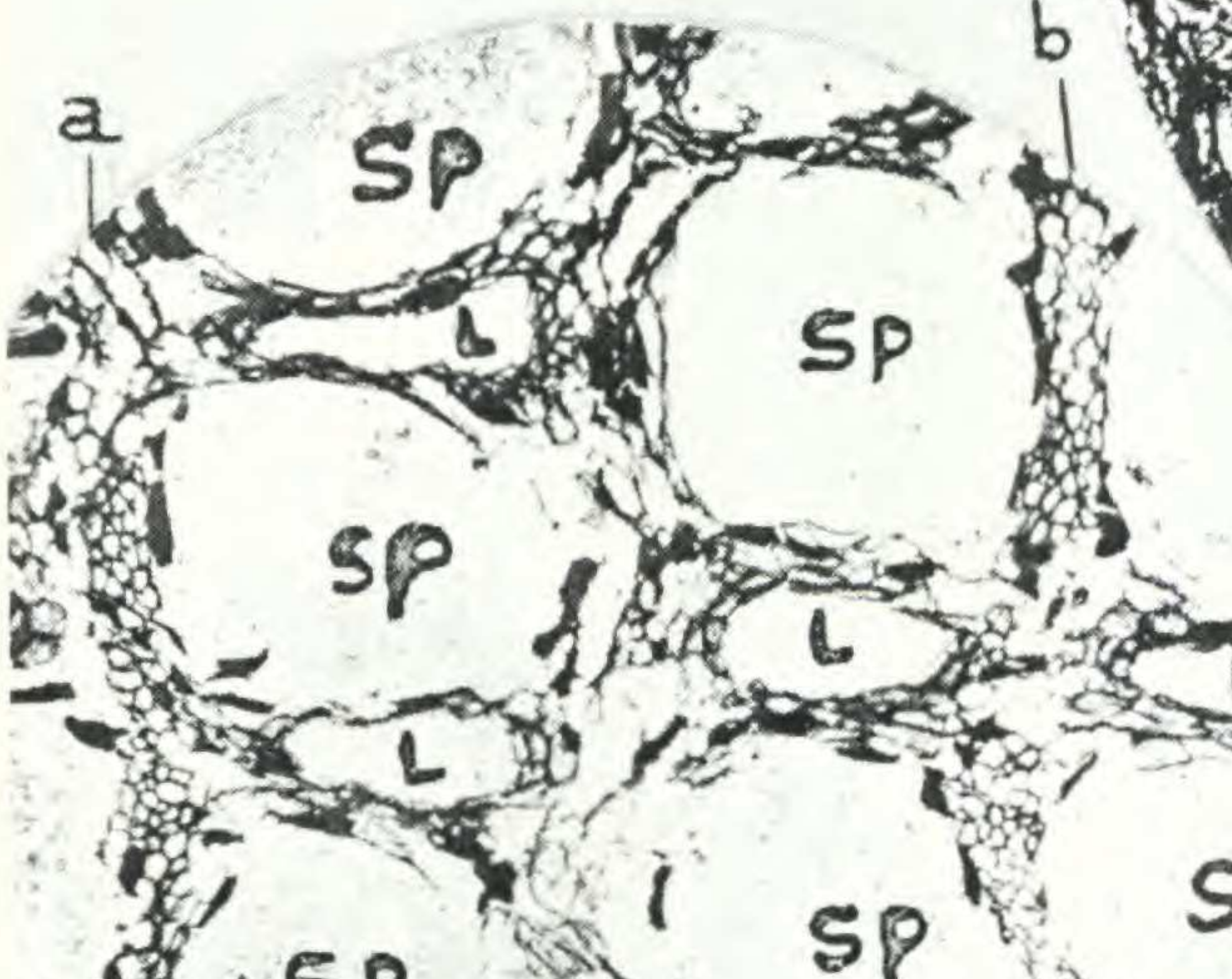

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BAXTER—FOSSIL PTERIDOSPERMS

Explanation of Plate

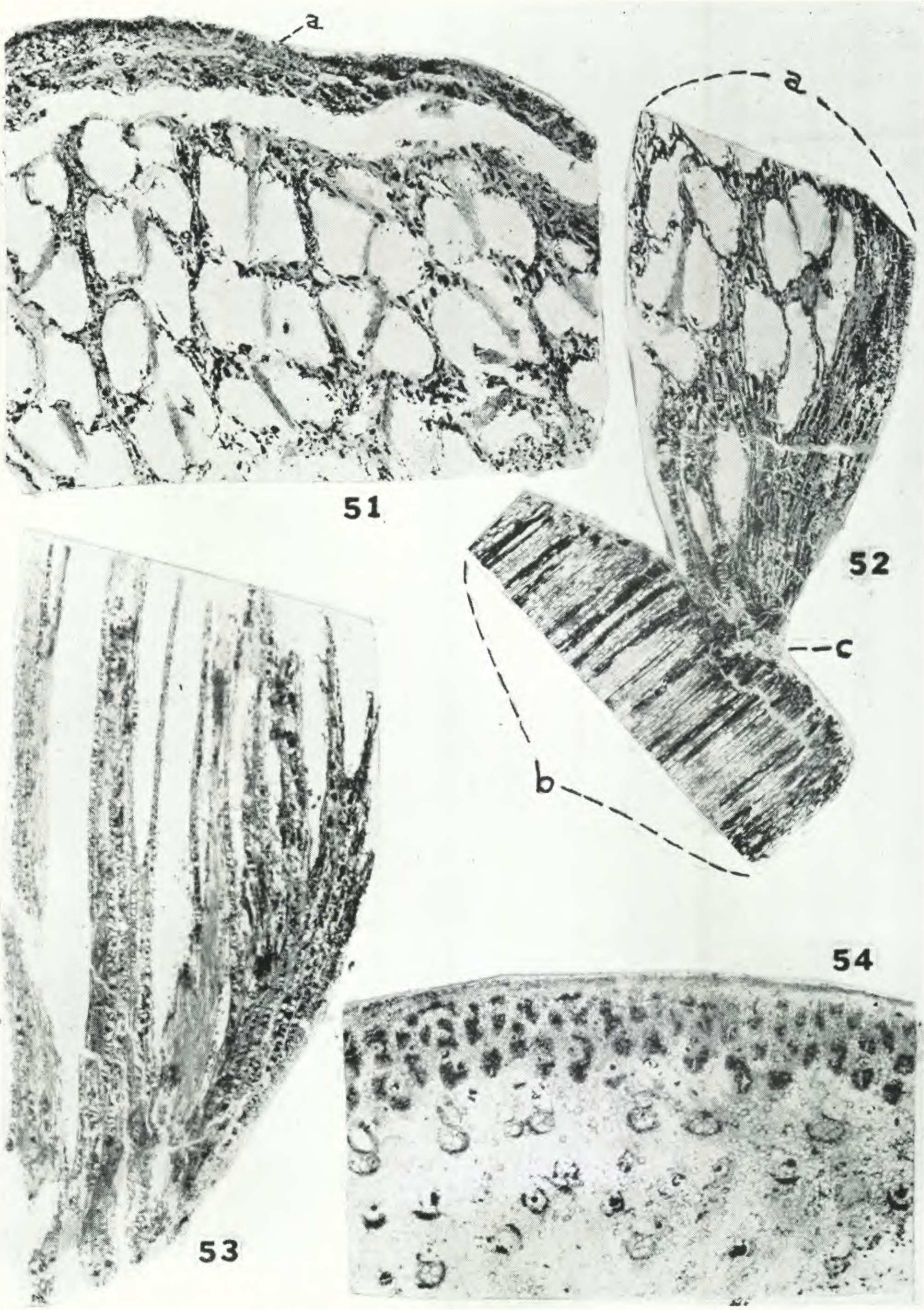
PLATE 16

Fig. 51. *Dolerotheca Schopfii.* Transverse view of marginal portion of campanulum: *a*, broad slime canal and sclerotic zone forming the wall of the fructification partly broken away from inner tissue. See figs. 46 and 47 for detail. From slide 1629, × 8.

Fig. 52. *Dolerotheca Schopfii: a*, oblique-longitudinal view showing possible attachment to *Myleoxylon* sp. at point indicated by *c*; *b*, longitudinal view of hypodermal zone of *Myleoxylon* sp. shown in fig. 54. From slide 1630, × 8.

Fig. 53. *Dolerotheca Schopfii.* Longitudinal view of marginal portion of campanulum showing the ascending origin of the outermost sporangia. From slide 1629, × 8.

Fig. 54. *Myleoxylon* sp. Transverse view of petiole shown in fig. 52b. From slide 1630, × 9.



BAXTER—FOSSIL PTERIDOSPERMS

EXPLANATION OF PLATE

PLATE 17

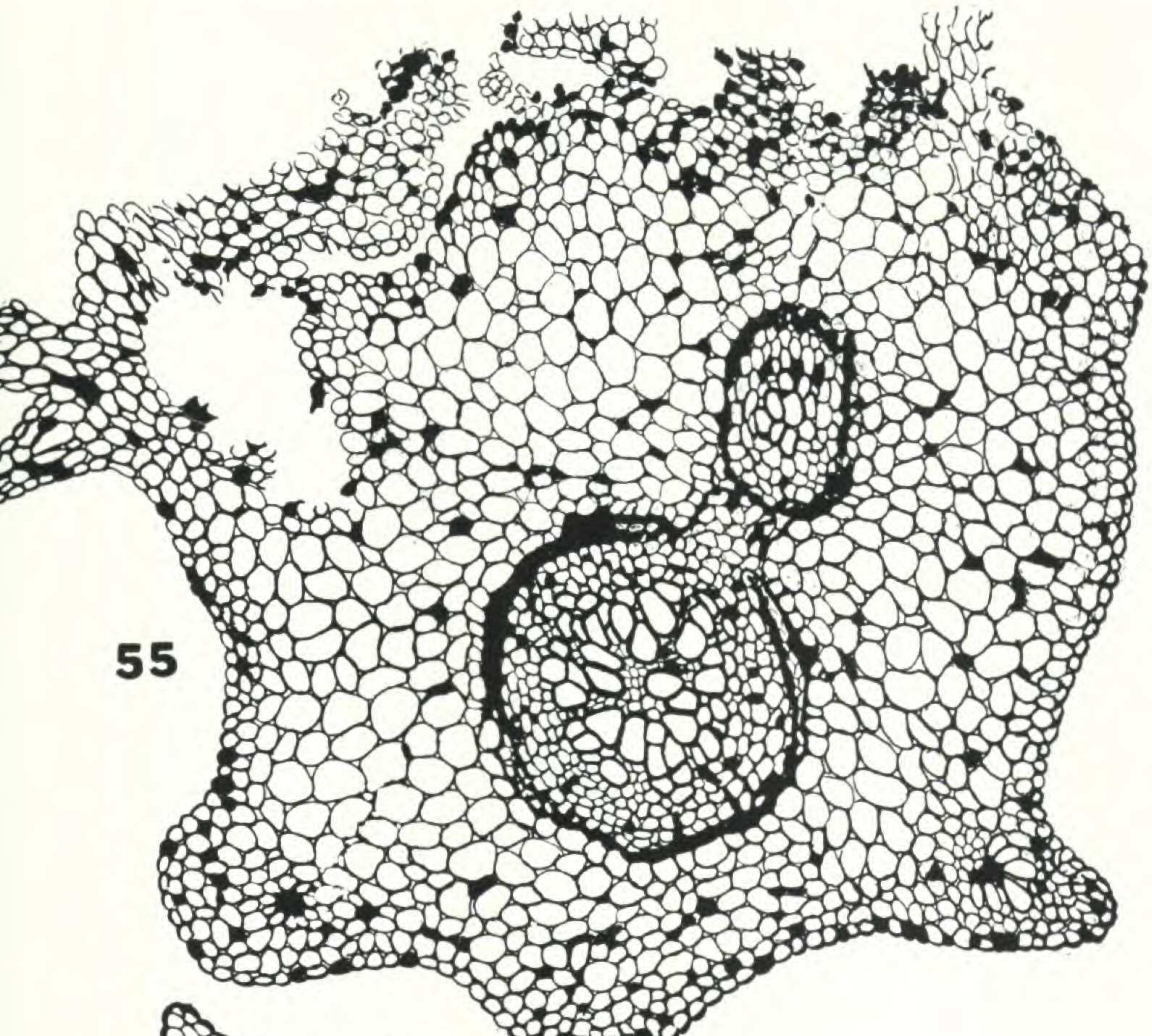
Fig. 55. *Microspermopteris aphyllum.* Cross-section of small stem or branch showing departure of branch bundle. This represents a stage shortly above that shown in fig. 3. From slide 1632, × 26.

Fig. 56. *Microspermopteris aphyllum.* Cross-section of an adventitious root. From slide 1633, × 34.

Fig. 57. *Dolerotheca Schopfii.* Drawing of epidermal hairs. From slide 1629, × 350.

Fig. 58. *Dolerotheca sclerotica.* Drawing of one of the rare glandular epidermal hairs. From slide 1631, × 550.

Fig. 59. *Medullosa Thompsonii.* Diagram of central portion of the stem: *a*, stelar assembly; *b*, line of "aggregate leaf traces" at point just above the departure of a petiole as indicated by absence of hypodermal fiber strands shown at *c*. See fig. 30 for detail of a single "aggregate trace." From slide 1626, × 4.



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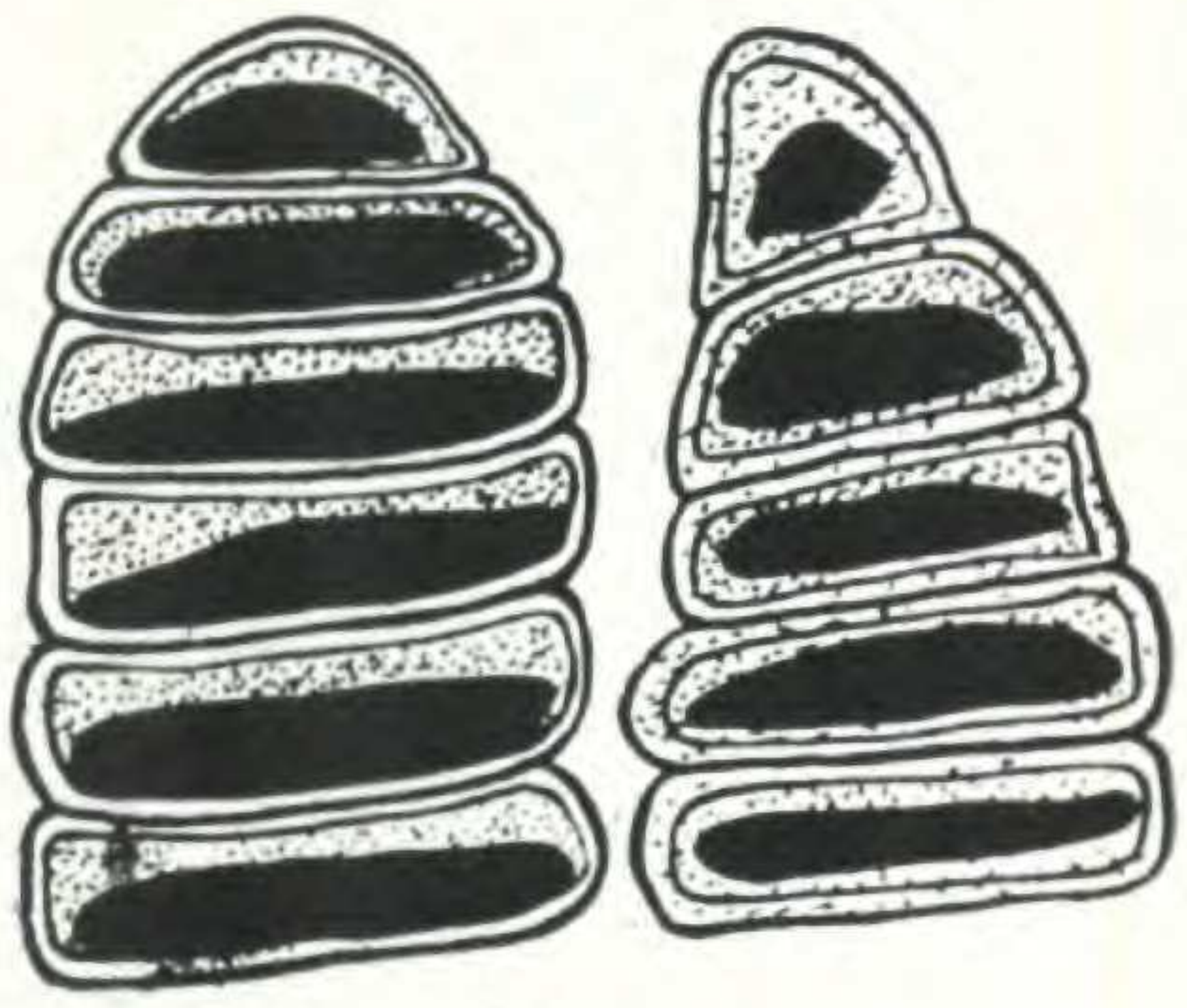

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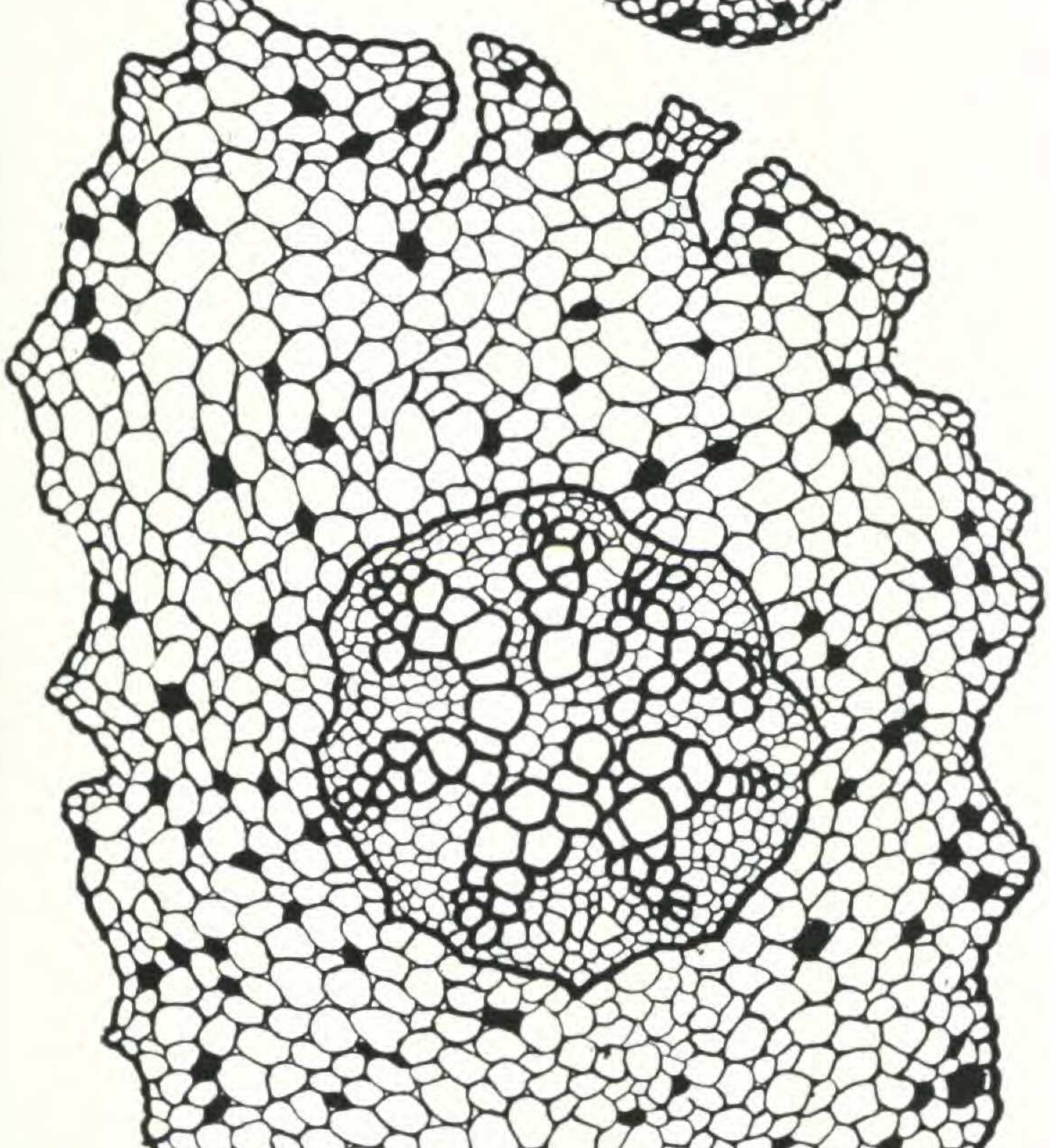

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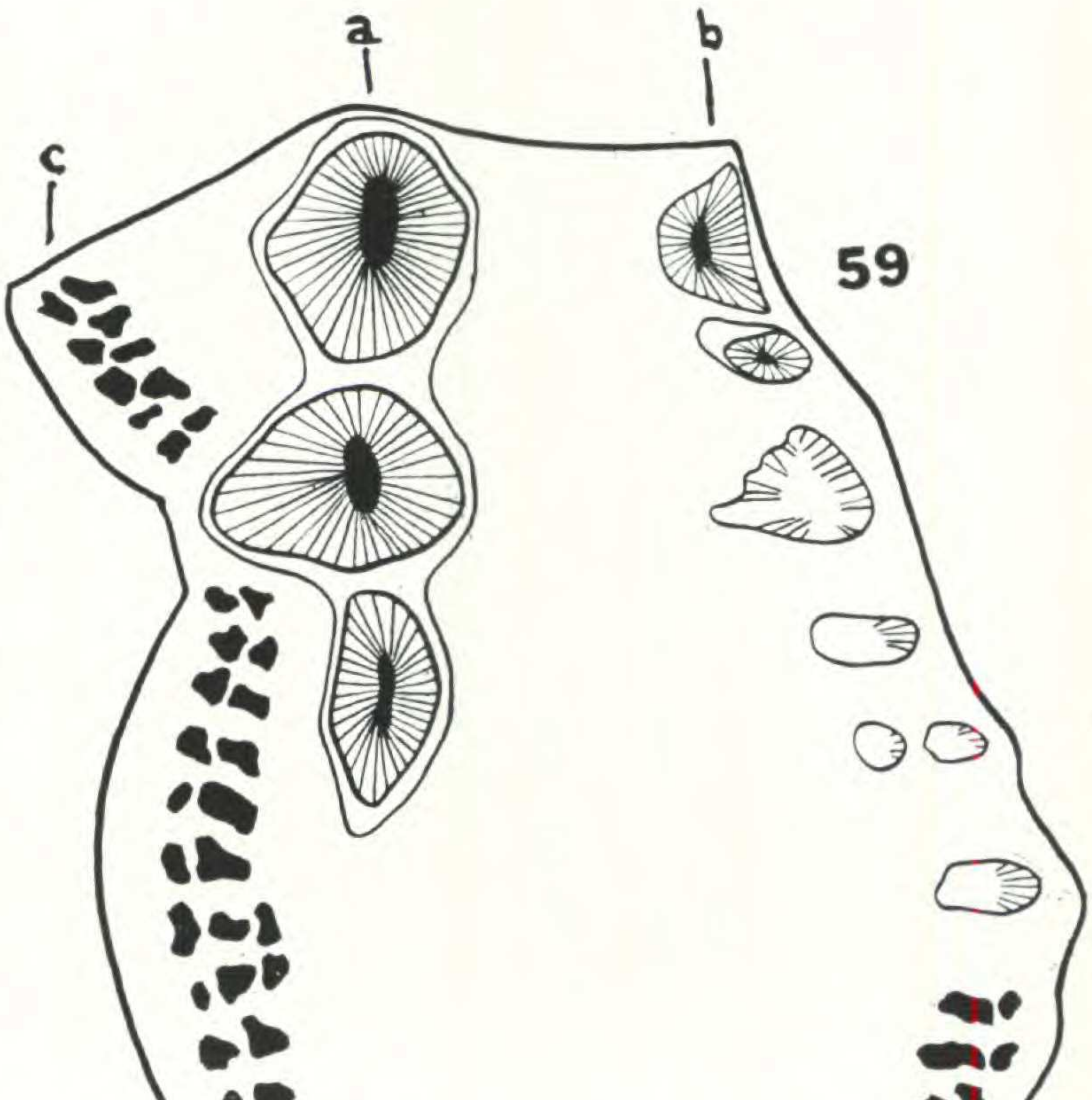

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